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Tadpoles of the Forested Regions of Borneo

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Tadpoles of the Forested Regions of Borneo

Abstract

Sixty-three forms of tadpoles are now known from Borneo, representing between 45% and 60% of the total anuran fauna. Fourteen of the larval forms cannot be assigned to species; a few of these clearly represent species, adults of which have not been recognized or discovered.

In general form, Bornean tadpoles vary from deep-bodied and spheroidal to flattened ovoid to extremely slender. Head-body lengths in late stages range from 3 to 36 mm, and denticle row counts, from 0/0 to 11/5. Denticles of most larval forms are spatulate, angled toward the mouth, and rimmed by 12 or more triangular cusps. In several forms the cusps are thin and elongate. Interspecific variation in the buccal cavity most often involves number, size, and disposition of projections from floor and roof, form of narial walls, and shape of ventral velum.

Bornean tadpoles live in at least 16 distinct kinds of microhabitats. Most forms have been found in two or three microhabitats, but several are apparently restricted to a single kind.

Introduction

Faunal works on the anurans of any tropical area usually have given short shrift to larvae, partly out of necessity because only relatively small, taxonomically narrow samples have been available and because many of the larval forms in collections cannot be (or have not been) assigned to species of adults with reasonable assurance. Another reason is that herpetologists have almost shunned anuran larvae as sources of taxonomical, ecological, and evolutionary information. I suspect this has occurred because, superficially, tadpoles have an even more circumscribed morphological compass than adults and because they are more difficult to manipulate as preserved specimens. After Noble's pioneering work (1927), only a few persons, among them notably Orton (1953, 1957) and Starrett (1973), have used tadpoles for broad systematic and phylogenetic studies. Recent work by Wassersug (1980) on the buccopharyngeal cavity of tadpoles has revealed a wide variety of structures that show strong interspecific variation, with clear taxonomic and ecological significance.

Both the relative neglect of larvae and recent evidence of their potential value in biological studies are part of the stimulus for this paper. Work in Borneo over the last 30 years led to the accumulation of a good collection of tadpoles. The problem of sample size mentioned at the outset is at least partially overcome. The large numbers of juveniles and adults collected at the same localities as the larvae have helped greatly in determining association of larval forms and adults. Detailed field notes on microhabitats for most of these Bornean larval samples give them an added biological interest.

Thirty-eight forms of larval anurans have been reported from Borneo in the century prior to 1984. In addition, tadpoles of four species that occur in Borneo have been described from other parts of their geographic ranges (Smith, 1916; Inger, 1960a; Berry, 1972; Kiew, 1973). Unfortunately, the

quality of these published descriptions varies widely. Some older ones, though adequate at the time of publication, are now too abbreviated, given the increase in knowledge and accumulation of specimens. Even some descriptions published within the last two decades are not satisfactory because they either do not cover enough characters or have not described characters in a consistent fashion. Furthermore, except for descriptions of the buccopharyngeal cavity of pelobatid larvae (Wassersug, 1980; Inger, 1983), we have no published information on features of the interior of the mouth. An additional weakness in the literature on Bornean tadpoles is the lack of detailed information on ecological distribution. Indeed, one can scarcely find such information for any large, tropical, amphibian fauna.

Sixty-three kinds of tadpoles are described in this paper, representing between 45% and 60% of the Bornean anuran fauna. The wide range of percentages is caused partly by the rapid increase in the size of the reported fauna (see papers by Iskandar, 1978; Inger & Frogner, 1980, Inger & Gritis, 1983; and Dring, 1983b) and partly by uncertainty over the inclusion of the genus *Philautus* which has no free-swimming tadpoles.

In this paper I present descriptions of the general external morphology and the internal buccopharyngeal anatomy, details of microhabitat distribution for each larval form (including occurrence with other larvae), the basis of association of each larval form with adults, and a key to the tadpoles of Borneo. Analysis of "community" structure for this assemblage of larval forms and discussion of diet and relationship of morphology to ecological distribution are being included in a separate publication (Inger, in preparation).

This work is part of a general effort to describe the fauna of the forests that, until relatively recently, covered all of Borneo. It, therefore, is an account of the indigenous anuran larvae of Borneo and does not include tadpoles of species that have recently invaded Borneo thanks to man's activities: *Bufo melanostictus, Kaloula pulchra, K. baleata, Rana cancrivora, R. erythraea, R. limnocharis, R. nicobariensis,* and *Polypedates leucomystax.* These eight commensals of man, abundant in agricultural areas and towns, use ponds, roadside ditches, paddy fields, and similar open situations for oviposition. Their larvae do not occur in Bornean forests. However, because they are likely to be encountered by students and to appear in shipments of tadpoles from "Borneo," they are referred to in footnotes at appropriate points in the key. Descriptions of these larvae have appeared in a number of publications (e.g., Flower, 1896; Smith, 1917; Kampen, 1923).

Despite the large samples of larvae, juveniles, and adults, 14 Bornean larval forms still cannot be assigned to species. All but two of these doubtful cases can be placed in genera with confidence. They represent two general kinds of problems. In some cases the tadpoles at hand have not developed far enough to permit recognition of diagnostic characters. For example, *Ansonia* sp. from Kinabalu (p. 20) is almost certainly the larva of one or the other of two sympatric species, but a decision between the two is not possible with the material available. In other cases, we have more distinguishable forms of larvae than species of adults. Larval *Amolops* are a good example of this kind of problem: there are eight distinguishable larval types, but only six species of adults are known from Borneo. Two of the unidentified larval forms cannot be assigned to genera, although their familial associations seem clear. One (p. 38) lacks keratinized mouth parts and has a median spiracle. It is obviously a microhylid larva, but the tadpoles lack diagnostic generic features. The second, taken from an artificial tree hole (p. 86), is almost certainly a rhacophorid larva, but the few individuals are all in early stages of development. All of the unassigned larvae are included in the key, with the hope that their inclusion will assist future work.

Materials and Methods

The descriptions and data rest primarily on the collections of Field Museum of Natural History (FMNH) supplemented by some tadpoles from the British Museum (Natural History) (BMNH). With few exceptions, specimens had been fixed in formalin. About half had been transferred to ethanol after a few months and have remained in alcohol for some years. Measurement and dissection of the buccopharyngeal cavity seem to be unaffected by these different treatments; the critical factor appears to be the quality of the initial fixation.

For most genera I present a complete description of external morphology for only one larval form and abbreviated descriptions of congeners, emphasizing those features that tend to vary among species. In a few genera, it seemed advisable to describe all forms completely. With few exceptions I give complete descriptions of the buccopharyngeal anatomy of every species dissected. My

rationale is that so little survey work has been done on this portion of larval morphology that we still have only a weak grasp of interspecific, intrageneric variation.

Descriptions of external morphology follow the sequence and definitions given in Inger & Frogner (1980). Measurements were made with an ocular grid, usually at 12× magnification. The sequence and terminology for buccopharyngeal morphology follow Wassersug (1980), except that "prelingual" and "prenarial" are used instead of "infralabial."

The microhabitats referred to in text have the following definitions: **Streams:** *Torrents*—surface of water broken, occasionally foaming, bed of rocks (diam. > 5 cm) and boulders, current strong. *Riffle*—surface of water in shallow waves but never foaming, bed of gravel and occasional rocks to ca. 25 cm, current moderate. *Shingle area*—surface of water smooth, bed of circular or oval, flattened rocks 3–10 cm, current weak to moderate. *Leaf drift*—areas of deep accumulation of dead leaves tightly packed except at periphery, drifts up to 1.5 m deep and 10 m long, current weak. *Open pool*—ponded parts of stream, current weak, bottom silt to sand and gravel. *Side pool*—an embayment off main channel, partially or completely cut off from current by sand or gravel bar, bottom fine to coarse sand and small gravel usually covered by dead leaves, current weak or absent. *Pothole on rock bank*—water-filled depression on rocky bank, bottom bed rock, though often with dead leaves, no current, potholes at varying heights above normal stream level. *Seepage area*—trickle of water less than 2 cm deep, usually emerging from steep clay bank. *Pool of intermittent stream*—up to 0.5 m in maximum surface dimension, depth to 5 cm, bottom fine silt, sand and pea-gravel, usually scattered dead leaves, no current except after moderate or heavy rain. **Microhabitats away from streams** (no current except in unusual circumstances): *Seepage area*—film of water less than 1 cm deep emerging from slope of clay and small rocks, current negligible. *Rain pool*—rain-filled depression of variable size and depth, bottom usually clay, often with dead leaves. *Animal wallow*—rain pool modified by action of mammals (mainly forest pigs, *Sus barbatus*), bottom fine silt, length more than 1 m, depth to 15 cm. *Log cavity*—mainly open on upper surface or side of log, surface up to 15 × 20 cm, depth to 10 cm. *Hole in living surface root*—small holes up to 18 cm in diameter and to 10 cm in depth, height above ground 5–16 cm. *Buttress tank*—cavity formed by anastomosis of two or more buttresses, surface area up to 30 × 40 cm, depth to 30 cm, height above ground to 4 m. *Hole in trunk or large branch*—surface area up to 20 × 30 cm, depth to 30 cm, height above ground of those searched 0.5–3 m.

Key to Bornean Tadpoles

Unless otherwise indicated, larval characteristics in the key are based on tadpoles in Stages 30–39. Only forms that are free-swimming at some interval are included.

1A. Without beaks; spiracle median ventral .. 54
B. With beaks; spiracle sinistral 2
2A. Without denticles 51
B. Denticles present on at least 1 lip 3
3A. A clearly defined abdominal suctorial disk occupying most of ventral surface of body 44
B. No abdominal suctorial disk 4
4A. At least 1 row of denticles on each lip .. 6
B. One lip lacking denticles 5
5A. No denticles on lower lip ..... *Pelophryne brevipes*
B. No denticles on upper lip ..... rhacophorid (genus?)
6A. Papillae confined to lateral thirds of both lips[1] 7
B. Papillae continuous across margin of lower lip or with narrow gap in center 10
7A. Rows of denticles on upper lip continuous 8
B. Inner row of upper denticles interrupted medially 9
8A. Posteroventral lobe of liver (visible through skin) curling superficially over rear of intestinal spiral, almost reaching midventral line ..... *Bufo asper*
B. Posteroventral lobe of liver not overlying intestinal spiral, well separated from midventral line ..... *Bufo divergens*
9A. Dorsal fin with melanophores at least in proximal fourth; rim of nostril with small, distinct middorsal projection ... *Bufo* sp.
B. Dorsal fin with melanophores only at its base; rim of nostril without projection ..... *Pedostibes hosei*

[1] Tadpoles of *Bufo melanostictus* are similar to larvae of *B. asper, B. divergens, Pedostibes hosei,* and *Bufo* sp. However, they differ from all of these forest forms in being heavily pigmented ventrally. The inner row of denticles on the upper lip is divided as in larval *P. hosei* and *Bufo* sp.

10A. No divided rows of denticles; 2 rows on upper lip, 3 on lower 11
B. At least 1 divided row of denticles; number of rows variable 14
11A. Upper beak narrowly divided, finely serrated ..... *Ansonia longidigita*
B. Median gap in upper beak wider than either piece, margin smooth 12
12A. No papillae on lower lip between marginal ones and rows of denticles; head-body with pattern of light and dark areas ..... *Ansonia albomaculata*
B. Low, rounded inframarginal papillae on lower lip; head-body uniformly dark dorsally and laterally 13
13A. Upper and lower rows of denticles subequal ..... *Ansonia minuta*
B. Upper rows of denticles much longer and curving around ends of lower ones ..... *Ansonia* sp.
14A. Only 1 row of denticles on upper lip[2] .. 15
B. More than 1 row of denticles on upper lip 16
15A. Distinct inframarginal papillae on lower lip ..... *Rana laticeps*
B. Only marginal papillae on lower lip ..... *Rana blythi*
16A. Only 1 undivided row of denticles on upper lip 17
B. At least 2 undivided rows on upper lip 39
17A. Outermost row of denticles on upper lip much shorter than adjacent row 18
B. Outermost row of denticles on upper lip subequal to or longer than next row .. 22
18A. Inframarginal ridges on lower lip without denticles ..... *Leptobrachium gracilis*
B. Inframarginal ridges with denticles ... 19
19A. Head-body and usually tail with small, round, black dots ..... *Leptobrachium hendricksoni*
B. Head-body never with pattern of small dots 20
20A. Head-body without markings ..... *Leptobrachium* sp. (Mulu)
B. Head-body with large, dark spots 21
21A. A dark transverse band across root of tail; in life, a middorsal stripe of gold flecks .. .. *Leptobrachium nigrops*
B. Head-body dark or olive with large, black spots; no transverse band at rear of body, though large spots often present there .... *Leptobrachium montanum*
22A. Only 2 rows of denticles on upper lip[3] 23
B. More than 2 rows of denticles on upper lip 25
23A. A distinct, median gap in papillae of lower lip ..... *Rana ibanorum*
B. Papillae continuous across lower lip, or if interrupted, gap not greater than width of 2 papillae 24
24A. Inframarginal papillae in lateral third of lower lip ..... *Rana kuhli*
B. No inframarginal papillae on lower lip ... .. *Rana ingeri, R. finchi, R. palavanensis*[4]
25A. Three rows of denticles on upper lip .. 26
B. More than 3 rows of denticles on upper lip 27
26A. Head-body and tail with dark spots ..... *Rana glandulosa*
B. Tadpole blackish, without spots ..... *Rana signata*
27A. Head-body with distinct glandular patches ..... *Rana chalconota*
B. Head-body without visible patches of glands 28
28A. Lower lip with 2 rows of denticles ..... *Rhacophorus* sp. D
B. Lower lip with 3 or 4 rows of denticles 29
29A. Tail divided into a lighter anterior half and a darker posterior half; the 2 areas separated by a vertical, thin, wavy line ..... *Rhacophorus dulitensis*
B. Pattern on tail otherwise 30
30A. Dorsal fin, and sometimes ventral, with distinct blackish margin ..... *Rhacophorus nigropalmatus*

[2] Larval *Rana nicobariensis* and *R. erythraea* agree with larval *R. blythi* and *R. laticeps* in number and relative lengths of denticle rows. However, the first two differ from *blythi* and *laticeps* in having distinctly elongated papillae on the lower lip.

[3] Tadpoles of *Rana limnocharis* and *R. cancrivora* resemble those of *R. ibanorum, R. kuhli, R. ingeri, R. finchi,* and *R. palavanensis* in number and relative lengths of rows of denticles. The first two are distinguished from *ibanorum* and its relatives by the coloration of the tail. In *limnocharis* the last third of the tail is very dark, contrasting sharply with the anterior portion. In *cancrivora* the muscle and both fins have large, round spots. From Stage 38 onward, larval *cancrivora* have a sharply defined, dark stripe on the developing hind limb.

[4] These larval forms are very similar externally. Assignment to species depends upon relatively complete developmental series (cf. pp. 42, 45, 52).

B. Tail fins without dark margins 31
31A. Dark crossband on head-body near root of tail 32
B. Head-body without dark crossband ... 33
32A. Dorsal fin with small, dark spots or reticulation ..... *Polypedates colletti*
B. Dorsal fin with dark bars continuous with dark blotches of caudal muscle ..... *Rhacophorus kajau*[5]
33A. Dark spots on side of snout and usually on other parts of head-body ..... *Rhacophorus pardalis*
B. Head-body without dark markings ... 34
34A. Tail uniformly dusky 35
B. Tail with distinct light spots 38
35A. Eyes lateral, visible from below 36
B. Eyes dorsolateral or dorsal, not visible from below 37
36A. Upper beak gently curved, a wide, weak median convexity[6] .... *Polypedates macrotis*
B. Upper beak with a strong, narrow median convexity ..... *Polypedates otilophus*
37A. Maximum width at midlength of head-body; eyes dorsolateral; interorbital about 1.5 times eye-snout ..... *Rhacophorus harrissoni*
B. Maximum width just behind eyes; eyes dorsal; interorbital about .75 of eye–snout ... . *Nyctixalus pictus*
38A. Dorsal fin thickened and not translucent proximally; caudal muscle deeper than dorsal fin in proximal half; head-body length >14 mm from Stage 36 onward ..... *Rana luctuosa*
B. Dorsal fin not thickened proximally, translucent throughout, deeper than caudal muscle beyond proximal third; head-body length <11 mm at all stages ..... *Rhacophorus appendiculatus*
39A. Upper lip with at least 8 rows of denticles ..... *Rhacophorus gauni*
B. Upper lip with 4 or 5 rows of denticles 40
40A. Papillae continuous across margin of upper lip; lower lip with 3–5 rows of papillae 41
B. Papillae of upper lip restricted to corners 42
41A. Lower lip with 1 divided and 2 continuous rows of denticles; outer surface of beaks ribbed ..... *Rhacophorus bimaculatus*
B. Lower lip with 4 or 5 continuous rows of denticles, no divided rows; outer surface of beaks smooth ..... *Rhacophorus* sp. KB
42A. Lower lip with 3 complete rows of papillae ..... *Rhacophorus* sp. NT
B. Lower lip with, at most, 2 rows of papillae 43
43A. Dark spots on snout and, usually, on other parts of head-body; 6 or 7 rows of denticles on upper lip ..... *Rhacophorus pardalis*
B. Head-body uniformly dark; 5 rows of denticles on upper lip ..... *Nyctixalus pictus*
44A. Beaks with smooth outer surface, keratinized portion of upper beak in one piece .. .. *Amolops cavitympanum*
B. Beaks with ribbed outer surface; keratinized portion of upper beak divided in two .. 45
45A. Lower beak divided 46
B. Lower beak in one piece 50
46A. More than 15 glands in cluster at end of body; no glands in ventral fin ..... *Amolops phaeomerus*
B. Less than 12 glands in cluster at end of body; usually a row of glands in ventral fin .. 47
47A. Head-body with flattened small protuberances laterally on snout and below eye ... . *Amolops* sp. G
B. Head-body with conical, spinule-like protuberances 48
48A. Spinules tipped with melanin ..... *Amolops* sp. H
B. Spinules whitish 49
49A. Lower lip usually with 4 undivided rows of denticles ..... *Amolops poecilus*
B. Lower lip usually with 6 undivided rows of denticles ..... *Amolops* sp. F
50A. Each half of upper beak with 11–19 coarse serrae, lower beak with 18–26 ..... *Amolops kinabaluensis*
B. Each half of upper beak with 5–9 serrae, lower beak with 11–16 ... *Amolops* sp. E
51A. Lips with continuous border of crowded papillae ..... *Leptobrachella mjobergi*
B. Lips without papillae 52
52A. Lips expanded into wide, funnel-like structure ..... *Megophrys nasuta*
B. Upper lip not distinguishable from snout or represented by narrow knob 53

[5] This dichotomy is uncertain. Information on *Rhacophorus kajau* is based on Dring (1983b).

[6] Larvae of *Polypedates leucomystax* are similar to those of *P. macrotis*. However, the former usually have only 3 divided rows of denticles on the upper lip (instead of 4), less deep bodies and tails, and the thickened basal portion of the ventral fin at least three times as long as deep (instead of twice as long).

53A. Both fins with distinct dark spots along margin ..... *Ooeidozyga laevis*
B. Ventral fin without marginal spots ..... *Ooeidozyga baluensis*
54A. Spiracle without flap, opening beneath center of intestinal spiral 55
B. Spiracle with movable flap, or opening at end of tube near anal tube[7] 57
55A. Gut with, at most, 2 or 3 complete coils .. .. *Kalophrynus pleurostigma*
B. Gut with numerous coils 56
56A. Tail tapered abruptly near end to rounded tip ..... *Chaperina fusca*
B. Tail tapering gradually to narrow tip .... microhylid (genus?)
57A. Lower lip expanded ..... *Microhyla* sp. C
B. Lower lip not expanded 58
58A. Tail tapering gradually from root into long, narrow filament ... *Microhyla borneensis*
B. Tail tapering abruptly in final fourth to short, narrow tip 59
59A. Fins without melanophores .... *Microhyla* sp. B
B. Fins crossed by broad, black, vertical band near tip 60
60A. Head-body with scattered melanophores ventrally; head-body length usually less than 4 mm (Stages 26–40) .. *Microhyla perparva*
B. Head-body without melanophores ventrally; head-body length usually greater than 4.0 mm ..... *Microhyla petrigena*

PELOBATIDAE

Leptobrachella mjobergi Smith

Association of these larvae with adults is based upon a developmental series culminating in a premetamorphic tadpole (Stage 41) having the distinctive triangular toe pads of this genus. Assignment to species is far less clear. In fact, probably several species are represented by the material included here. A tadpole from lowland eastern Sabah (FMNH 77503) differs from one from Mt. Kinabalu (FMNH 130861) in surface ornamentation of the ventral velum (Inger, 1983). Dring (1983a) argues that adults from these two areas represent two species, *L. parva* Dring and *L. baluensis* Smith, respectively, both of which are distinct from *L. mjobergi* Smith of southern and western Sarawak, the source of most of the material I have examined. Unfortunately, these samples are not large enough to build a substantial case for differentiation among the larvae.

A complete description has recently been published (Inger, 1983). I give only an abbreviated one here.

DESCRIPTION—**External**—Head-body extremely elongate, width .31–.36 of head-body length, depth .80–.85 of head-body width; eyes dorsolateral, eyeball increasing with stage of development, .03 of head-body length (Stage 25), .04 (Stage 31), .07 (Stage 36), .10 (Stage 41); interorbital .25–.31 of head-body width. Oral disk ventral, subterminal, cuplike with expanded lips; width of disk .42–.44 of head-body width; short papillae in single continuous series around entire margin of lips; beaks heavy, fully pigmented, finely serrated. Spiracle midlateral, tube free of body wall, snout–spiracle .45–.48 of head-body length. Tail heavy, almost as wide as body in proximal third; tail length 1.7–2.1 times head-body length, maximum depth .15–.18 of tail length; fins very narrow. Entire tadpole pinkish gray in life. Head-body lengths 11.5–13.5 mm (Stages 35–37).

Internal Buccopharyngeal (based on FMNH 77503, Stage 36, and FMNH 130861, Stage 30)—Prelingual area of floor with 2 pairs of thick palps. Tongue anlage low, without papillae. Buccal floor arena with 10–12 long, simple papillae on each lateral border; interior with 3–4 short papillae in midline anteriorly, followed by 20–30 low pustules on each side. Ventral velum wide, without spicules; dorsal surface with 2 groups of pustules narrowly separated in midline; a deep median notch; median lobe of each side divided horizontally, dorsal portion with 2 long papillae and ventral portion with 10 or more; lateral lobes with 2–3 short marginal papillae. Glottis under median notch of velum. Only 1 filter cavity on each side; no ruffled filter surface.

Prenarial region of roof bounded at rear by 4 short papillae. Nares obliquely oval, thin walls with 1 or 2 pustules. Lateral ridge papilla with 2 long branches. Median ridge with 3 triangular lobes. Buccal roof arena with about 40 pointed papillae followed by wide, transverse band of ca. 100 pustules. Dorsal velum with 15–20 long marginal projections on each side.

ECOLOGICAL DISTRIBUTION—Larval *Leptobrachella* appears to be limited to areas of moderate current over gravel beds within which these larvae live. This habit probably isolates them from

[7] Tadpoles of *Kaloula pulchra* and *K. baleata* differ from all other Bornean microhylid larvae in having the spiracular opening at the end of the body overlying the anal tube.

TABLE 1. Microhabitat distribution of larval *Leptobrachella mjobergi* in forest streams and their occurrence with tadpoles of other species.

Species	No. of samples	
	Riffle	Shingle
Leptobrachium gracilis	2	...
Leptobrachium montanum	...	1
Megophrys nasuta	1	2
Rana signata	1	...
Rhacophorus bimaculatus	1	2
Without other tadpoles	2	0
Total samples	4	2

all other tadpoles except those of *Leptobrachium gracilis,* though altogether five kinds of larvae were taken in the same collections (table 1).

REFERRED MATERIAL—FMNH 77503–4, Deramakot, Kinabatangan District, Sabah; FMNH 130861–3, Sungei Kepungit, Mt. Kinabalu, Sabah; FMNH 157998, Sungei Pesu, Tubau district, Fourth Division, Sarawak; FMNH 77515, Nanga Putai, Baleh River, Seventh Division, Sarawak; FMNH 212384–5, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Leptobrachium

Tadpoles of Bornean species are moderately large—head-body lengths more than 20 mm at Stage 30 and beyond (table 2). All have a continuous fringe of short papillae around both lips; heavy, black, V-shaped beaks; outermost row of denticles on both lips very short; at least 4 divided rows of denticles on the upper lip (Stage 30 and beyond); compressed, curved, pointed denticles (fig. 1); and short oblique ridges laterally on the lower lip between the marginal papillae and rows of denticles. Larval *L. gracilis* are relatively slender, whereas those of *hendricksoni, montanum,* and *nigrops* are robust.

As a detailed description of larval *L. montanum* has been published recently (Inger, 1983), I give only an abbreviated description of its external morphology and compare the other larvae to that standard.

Leptobrachium montanum Fischer

Association with adults is based upon a complete developmental series (Stages 25–41). The older larvae have the coloration of adults on the fully developed hind limbs, lack the dotted pattern of *hendricksoni,* and have blunt fingertips, as in adult *montanum,* instead of the sharply pointed fingers characteristic of *nigrops.*

DESCRIPTION—**External**—Head-body robust, width .54–.66 of head-body length, depth .74–.81 of head-body width; eyes dorsolateral, eyeball .10–.11 of head-body length (Stages 27–39); interorbital .40–.50 of head-body width. Oral disk ventral, subterminal; width of disk .36–.48 of head-body width; denticles I:5+5 or I:6+6 on upper lip, 5+5:I on lower; lateral inframarginal ridges with small denticles; beaks heavy, fully pigmented, coarsely serrated. Spiracle midlateral, tube fused to body wall; snout–spiracle .56–.61 of head-body length. Tail weakly convex; tail length 1.6–1.9 times head-body length, maximum depth .31–.38 of tail length. Lateral line pores visible. Three small, whitish, glandular patches ventrally on each side near end of body.

Olive in life, with large dark spots on head-body and tail; spots increase in size with development. In preservative markings often become obscured. Head-body lengths in Table 2. Total length to 73.6 mm (Stage 41).

Internal Buccopharyngeal (based on FMNH 63537, Stage 36, and FMNH 139380, Stage 37, both examined by means of SEM; FMNH 63537, Stage 37)—Prelingual area of floor with 2 pairs of branched palps on each side; a pair of conical pa-

TABLE 2. Size variation (head-body length in mm) of larval *Leptobrachium* from Borneo. Sample size in parentheses.

Species	Stages			
	26-29	30-33	34-37	38-41
gracilis	15.3–20.2 (4)	...	21.7 (2)	...
hendricksoni	24.2–27.2 (5)	26.3–28.3 (2)	29.2–34.4 (4)	29.0–35.7 (4)
montanum	16.2–19.5 (8)	20.5–22.7 (3)	21.0–26.7 (5)	22.2–27.7 (4)
nigrops	...*	24.5–26.7 (2)	...	...
sp. (Mt. Mulu)	...	24.0 (1)	...	...

* Three larvae of *nigrops* in Stage 25 exceeded 16.5 mm.

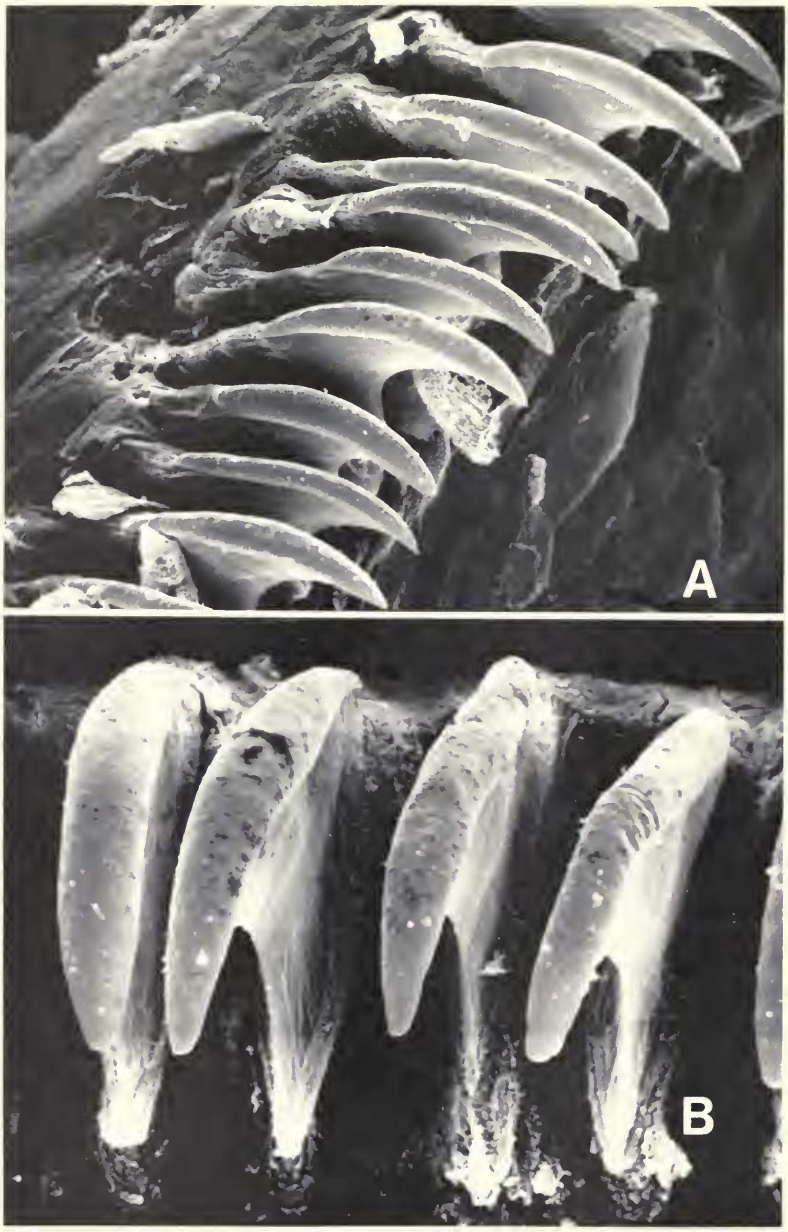

FIG. 1. *Leptobrachium montanum.* **A,** Denticles of outermost divided row of upper lip, oblique view (× 1,000); **B,** denticles of same row, ventral view (× 2,000).

pillae medially between posterior palps (analogues of lingual papillae?). Tongue anlage indistinct. Buccal floor arena (fig. 2) with 10–13 large papillae on each lateral border, third to tenth branched; interior of arena with ca. 100 low pustules, densest posteriorly and extending on to velum. Buccal pockets transverse, curved; a row of 6–7 short papillae posteromesad from pockets, curving behind last floor arena papillae. Ventral velum supported by spicules; dorsal surface medially with pustules; laterally margin with 2 or 3 shallow curves marked by short projections; median portion of velum set off by notches, with 2 pairs of large knobby or pustulose papillae from dorsal edge and a pair of short papillae from ventral edge; median portion of velum with secretory pits. Glottis exposed be-

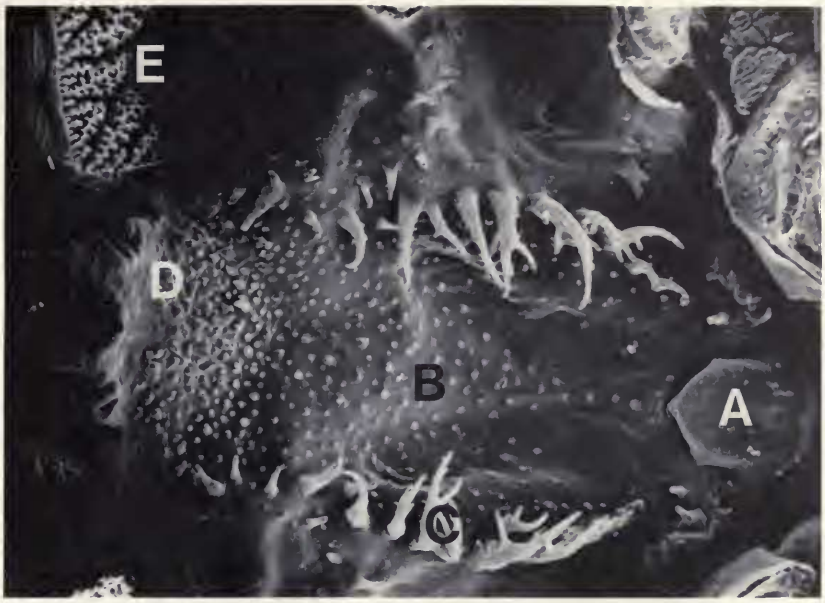

FIG. 2. *Leptobrachium montanum.* Floor of mouth, anterior to right (× 24). **A,** Tongue anlage; **B,** buccal floor arena; **C,** lateral papillae of buccal floor arena; **D,** ventral velum; **E,** branchial basket of left side.

hind velum. Three gill chambers on each side; filter ruffles with tertiary folds; 7–11 filter rows on median wall of middle chamber.

Prenarial area of roof with 1 pair of slender papillae. Nares oval, transverse; anterior narial wall with 1 curved papilla laterally; posterior wall higher, with 1 long, curved papilla medially. Postnarial area with 3–6 papillae in transverse rows on each side. Lateral ridge papilla long, bifurcate. Median ridge triangular. Buccal roof arena with 8–10 long papillae laterally in staggered row, inner ones with short branches; interior of arena with many short papillae and pustules. Glandular zone widest medially. Dorsal velum with ca. 12 projections on each side, medial ones longest.

ECOLOGICAL DISTRIBUTION—Larval *L. montanum* is concentrated in stream microhabitats with weak or moderate currents (see Inger, 1966, fig. 10). In these situations they have been collected with a variety of other kinds of tadpoles (table 3).

REFERRED MATERIAL—FMNH 63531–41, Bukit Kretam, Sandakan District, Sabah; FMNH 77220, Sepilok Forest Reserve, Sandakan District, Sabah; FMNH 77519, Deramakot, Kinabatangan District, Sabah; FMNH 77221–2, 77518, Kalabakan, Tawau District, Sabah; FMNH 140216, 6 km E. of Tuaran, Sabah; FMNH 130858–9, Sungei Kepungit, Mt. Kinabalu, Sabah; FMNH 131244, Sungei Liwagu, Mt. Kinabalu, Sabah; FMNH 130857, Sungei Matukungan, Mt. Kinabalu, Sabah; FMNH 121858, Gunong Temiang, Sungei Sabambam, First Division, Sarawak; FMNH 83018, Sungei Paloh, Patah River, Fourth Division, Sarawak; FMNH 83017, Long Seniai, Akah River, Fourth Division, Sarawak; FMNH 77517, 77578, Nanga Putai, Baleh River, Seventh Division, Sarawak; FMNH 96022, headwaters of Baleh River, Seventh Division, Sarawak; FMNH 139375–80, 148286, 212388–91, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Leptobrachium gracilis Günther

Association of this larval form with adults is based upon a developmental series from Stage 25 through metamorphic stages (41–45). The toes of advanced larvae and transforming individuals have the long callous ridges characteristic of this species, and the oldest members of the series are clearly conspecific with other juveniles of *L. gracilis.*

DESCRIPTION—**External**—Head-body an elongate oval. Head-body width .42–.51 of head-body length; depth .70–.75 of head-body width; eyeball .03–.04 of head-body length (Stages 25–27), .05–.07 (Stages 34–37); width of oral disk .39–.45 of head-body width; snout–spiracle .48–.52 of head-body length; tail length 1.7–2.2 times head-body length, maximum depth .20–.25 of tail length. Oral disk with expanded cuplike lips; inframarginal ridges of lower lip without small denticles; den-

TABLE 3. Microhabitat distribution of larval *Leptobrachium montanum* in forest streams and their occurrence with tadpoles of other species.

Species	No. of samples				
	Torrent	Riffle	Shingle	Open pool	Protected side pool
Leptobrachium gracilis	...	1	...	...	...
Leptobrachella mjobergi	...	1	...	...	...
Megophrys nasuta	...	1	1	...	...
Bufo divergens	...	...	...	...	1
Pedostibes hosei	...	...	...	...	1
Amolops cavitympanum	1	...	...	...	...
Amolops phaeomerus	1	1	...	...	...
Amolops poecilus	1	...	...	...	...
Rana blythi	...	...	...	2	2
Rana chalconota	...	...	...	1	2
Rana ibanorum	...	...	1	...	...
Rana signata	...	...	...	...	1
Rhacophorus bimaculatus	...	1	2	...	...
Without other tadpoles	0	1	0	10	0
Total samples	1	2	2	12	3

ticles on upper lip I:3+3 to I:4+4 (Stage 26), I:4+4 to I:6+6 (Stages 27–37); 2+2:I on lower lip (Stages 26–37); beaks finely serrated. Spiracular tube free of body wall near tip. Tail with heavy muscle and low fins. Entire tadpole pinkish gray in life, without pattern. Head-body lengths in Table 2. Total length to 64.6 mm (Stage 35).

Internal Buccopharyngeal (based on FMNH 146323, Stage 35, examined by means of SEM)—Prelingual area of floor with 2 pairs of thick palps. Tongue anlage low, a pair of conical lingual papillae. Buccal floor arena with 8–9 papillae on each lateral border; interior with 3 median papillae followed by about 40 pustules in transverse band. Ventral velum wide, without spicules; dorsal surface medially with pustules continuous with those of buccal floor arena and interrupted in midline; a deep median notch; median area of velum divided horizontally, dorsal portion bearing 2 pairs of papillae and ventral portion with about 20 filamentous papillae on each side; lateral portion of velum without papillae. Glottis under median velar papillae. Three gill chambers on each side; filter rows with tertiary folds; canals open.

Prenarial area of roof with 1 pair of low papillae. Nares transversely oval; widely separated; with thin walls; anterior wall pustulose, posterior with 1 long papilla medially. Postnarial area with 3 triangular papillae on each side. Lateral ridge palp triangular, bifurcate at tip. Median ridge divided into 3 triangular lobes. Buccal roof arena with about 30 pointed papillae followed by wide transverse band of many pustules. Dorsal velum with 18–20 long marginal projections on both sides.

ECOLOGICAL DISTRIBUTION—Restricted to areas of moderate to swift current in clear streams. Although a variety of other kinds of tadpoles were taken with these samples (table 4), larval *gracilis* may actually co-occur only with those of *Leptobrachella* because only these two types appear to wriggle into the interstices of gravel beds.

REFERRED MATERIAL—FMNH 212382, Deramakot, Kinabatangan District, Sabah; FMNH 130860, 212381, Sungei Kepungit, Mt. Kinabalu, Sabah; FMNH 131245–6, Sungei Liwagu, Mt. Kinabalu, Sabah; FMNH 130864, Sungei Mamut, Mt. Kinabalu, Sabah; FMNH 77509, 77511, Matang, First Division, Sarawak; FMNH 77516,

TABLE 4. Microhabitat distribution of larval *Leptobrachium gracilis* in forest streams and their association with tadpoles of other species.

Species	No. of samples	
	Torrent	Riffle
Leptobrachella mjobergi	...	2
Leptobrachium montanum	...	1
Megophrys nasuta	...	2
Amolops phaeomerus	...	1
Rana signata	...	1
Rhacophorus bimaculatus	...	2
Without other tadpoles	1	2
Total samples	1	4

Nanga Putai, Baleh River, Seventh Division, Sarawak; FMNH 139381, 146323, 146341, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Leptobrachium hendricksoni Taylor

Association of these larvae with adults is based on a complete developmental series from pre-limb bud to metamorphic stages (Stage 45). At all stages the larvae have the distinctive dotted pattern that characterizes adult *L. hendricksoni* and distinguishes it from all other Bornean frogs.

DESCRIPTION—**External**—Robust, generally similar in form to larval *L. montanum.* Head-body width .54–.66 of head-body length, depth .71–.76 of head-body width; eyeball .09–.12 of head-body length (Stages 31–39); interorbital .36–.37 of head-body width; width of oral disk .33–.37 of head-body width; snout–spiracle .47–.59 of head-body length; tail length 1.3–1.7 times head-body length, maximum depth .27–.30 of tail length. Oral disk similar in shape to that of *L. montanum*; denticles in Stages 30 onward I:6+6 or I:7+7 on upper lip; 6+6:I or, rarely, 5+5:I on lower lip; lateral inframarginal ridges of lower lip with small denticles; beaks with coarse serrations. Body without glandular patches posteroventrally. Reddish brown or pinkish in preservative, with numerous small black dots on all surfaces.

Head-body lengths in Table 2. Total length to 76.5 mm (Stage 36).

Internal Buccopharyngeal (based on FMNH 148283, Stage 32)—Prelingual area of floor with 2 pairs of large papillae, the posterior ones branched. Tongue anlage low; a pair of lingual papillae. Buccal floor arena with 10–12 long papillae on each lateral border; an interior row of 8 short papillae on each side; a band of about 12 short papillae across posterior border. Ventral velum wide, with spicules; dorsal surface medially with about 50 pustules in an undivided group; velum divided into median and lateral portions by wide notch on each side; median portion with 4 long, thick papillae dorsally and 2 triangular projections ventrally; each lateral portion of velum with 6 short marginal projections; secretory pits on margin of velum and on median papillae. Glottis behind velar margin. Three gill chambers on each side; filter rows with tertiary folds, canals open.

Prenarial area of roof with 2 low pustules on each side. Nares transversely oval, well separated; anterior wall laterally with 1 tall papilla; posterior wall with a similar papilla medially. Postnarial area with 3 papillae in a transverse row on each side. Lateral ridge papilla longer than narial papillae, curved, bifurcate at tip. Median ridge semilunar, margin with low projections, half height of lateral ridge papilla. Buccal roof arena with 8–12 papillae on each lateral border; a row of shorter papillae just outside lateral row; central area with many pustules. Glandular zone 3–5 pits wide laterally, narrowing to single row medially. Dorsal velum with 7–9 projections on each side.

ECOLOGICAL DISTRIBUTION—Appears to be limited to areas of weak current in streams—1 sample from a protected side pool and 2 from slow, open pools. No other kinds of larvae were captured with these 3 samples.

REFERRED MATERIAL—FMNH 119898–9, 129016, Subis Forest Reserve, Niah; FMNH 148282–3, Labang, Kemena River; FMNH 158215–8, Sungei Pesu, Tubau district. All in the Fourth Division, Sarawak.

Leptobrachium nigrops Berry and Hendrickson

Association with adults is not certain. None of these larvae, which differ from those of *L. gracilis, hendricksoni,* and *montanum* in coloration, was sufficiently mature to have digits at a stage allowing definitive comparison with adult *L. nigrops.* Adults of *nigrops* were collected at only four sites—Nyabau, Labang, Sungei Pesu, and Nanga Putai, all in lowland Sarawak. Larvae having the distinctive golden middorsal stripe were found only at Nyabau and S. Pesu. Adult and larval *hendricksoni* were caught at Labang and S. Pesu, and adult but not larval *montanum,* at Nyabau and Labang. Adults and larvae of the last species were collected at Nanga Tekalit, Sarawak, and at several localities in Sabah. Assignment of the gold-striped tadpoles to *L. nigrops* is based, therefore, on a process of elimination and occurrence of larvae where adults were also found.

These gold-striped tadpoles appear to have more rows of denticles than Sarawak larvae of *L. montanum* (table 5). They also differ markedly from Malayan larvae assigned to *nigrops* by Berry (1972) in body shape, coloration, and number of rows of denticles.

DESCRIPTION—**External**—Similar in general form to larval *L. montanum.* Head-body width .63–.69 of head-body length, depth .75–.80 of head-body width; eyeball .09–.13 of head-body length (Stages 31–38); width of oral disk .34–.36 of head-body width; snout–spiracle .53–.60 of head-body

TABLE 5. Number of divided rows of denticles in larval *Leptobrachium montanum* and *L. nigrops* from Sarawak. All larvae in Stages 25–33 and with head-body lengths greater than 12.5 mm.

	No. of tadpoles			
	Upper lip		Lower lip	
Species	N = 5	N = 6	N = 4	N = 5
Leptobrachium montanum	6	8	9	5
Leptobrachium nigrops	1	9	1	9

N = Number of divided rows.

length; tail length 1.4–1.8 times head-body length. Oral disk similar in shape to that of larval *L. montanum*; denticles usually I:6+6/5+5:I (table 5); lateral inframarginal ridges of lower lip with small denticles; beaks coarsely serrated. Body usually with small whitish glandular patches posteroventrally. Color in life pale yellowish with a middorsal stripe of gold flecks, a broad dark transverse band at rear of body, and a narrow dark interorbital bar. In preservative, golden stripe usually replaced by an irregular dark streak.

Head-body lengths in Table 2. Total length to 73.3 mm (Stage 31).

Internal Buccopharyngeal (based on FMNH 77513, Stage 26, and FMNH 148285, Stage 31; latter examined by means of SEM)—Prelingual area of floor with a large multibranched palp in each posterolateral corner, preceded by a slightly smaller one; branches of palps longer and thinner in FMNH 148285. Tongue anlage low; a pair of conical lingual papillae between posterior prelingual palps. Lateral to swelling of tongue anlage and anterior to level of buccal floor arena a low, thick, transverse ridge bearing several short papillae. Buccal floor arena with 8–11 long papillae in staggered row on each lateral border, 4 or 5 in middle branched; interior with 50–100 low pustules. Ventral velum deep, with spicules; dorsal surface medially with ca. 50 low pustules in single group; velum divided into median and lateral portions by notch; median portion with 2 pairs of large, thick papillae from dorsal edge, 1 pair of shorter papillae ventrally; papillae and margin of velum with secretory pits. Glottis exposed between median velar papillae. Three gill chambers on each side; filter rows with tertiary folds; canals open.

Prenarial area of roof with large 3-branched papilla behind lateral corner of beak. Nares transversely oval, well separated; anterior wall low, with tall papilla rising from lateral portion, papilla with 1 short branch or pustule; posterior narial wall higher, with short, curved papilla at its median corner. Postnarial area with 5–8 long papillae in 2 oblique rows on each side. Lateral ridge papilla long, bifid at tip and with short branch or pustule near base. Median ridge triangular, margin pustulose. Buccal roof arena with 8–12 long papillae in staggered row on each lateral border, several branched; interior with 6–12 short papillae anteriorly, rest of area with ca. 100 pustules extending behind level of lateral papillae. Glandular zone continuous across roof, narrow, 1 or 2 pits deep. Dorsal velum with 9–11 long, pustulose projections on each side.

ECOLOGICAL DISTRIBUTION—Limited to slowly flowing water. Four samples were obtained in open pools of a slow, small stream, and 3 from small protected side pools. Only 1 of the samples, from a side pool, included other larvae—4 *Rana blythi,* 10 *R. kuhli,* and 9 *Polypedates colletti.*

REFERRED MATERIAL—FMNH 148284–5, 151515–20, 158209–10, Nyabau, Bintulu District, Fourth Division, Sarawak; FMNH 158211–4, Sungei Pesu, Tubau district, Fourth Division, Sarawak; FMNH 77512–3, 77578, Nanga Putai, Baleh River, Seventh Division, Sarawak.

Leptobrachium sp.

Three larvae, collected at 1,800 m on Mt. Mulu, resemble larval *L. gracilis* in having a uniform coloration and a relatively slender body (width of head-body less than .5 of its length). However, in other respects they resemble larval *L. montanum, hendricksoni,* and *nigrops*: inframarginal ridges of lower lip with small denticles, only 3 pairs of long papillae projecting back from median portion of ventral velum. Almost certainly they represent a new species, adults of which have not been discovered.

DESCRIPTION—**External**—General shape as in larval *L. gracilis,* oral disk as in larval *montanum.* Head-body width .47 of head-body length; eyeball .07 of head-body length (Stage 26); interorbital .43 of head-body width; tail length 1.8 times head-body length, maximum depth .27 of tail length. Lips as in larval *montanum*; denticles I:6+6/4+4:I (Stage 26) and I:6+6/5+4:I (stage 25); spiracular tube free at very tip. Small, whitish, glandular patches on body posteroventrally. In preservative dark gray, without pattern. Head-body length (mm): 15.8, 19.3 (Stage 25), 24.0 (Stage 26). Total length to 66.5 mm (Stage 26).

Internal Buccopharyngeal (based on BMNH 1978.1526, Stage 25)—Two conical lingual pa-

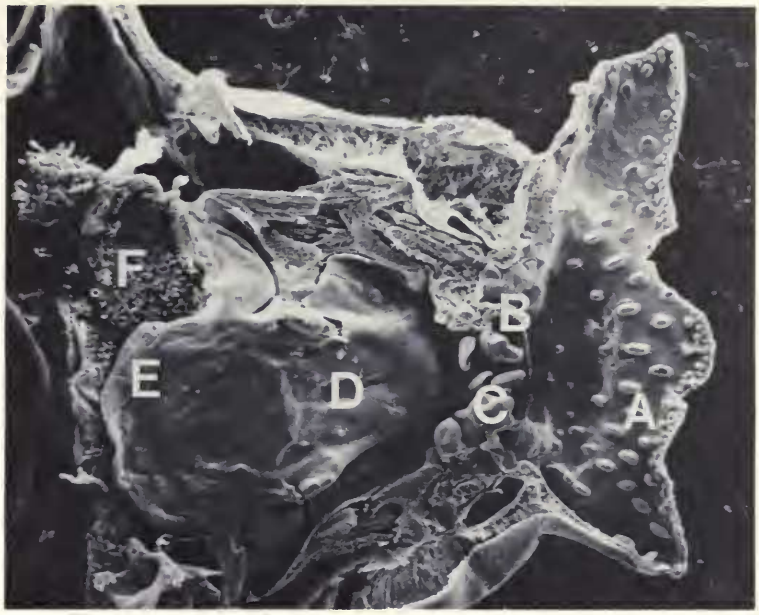

FIG. 3. *Megophrys nasuta.* Lower lip and floor of mouth (× 22), anterior to right. **A,** Lower lip; **B,** beak; **C,** prelingual palps; **D,** buccal floor arena; **E,** ventral velum; **F,** branchial basket of left side.

pillae. Buccal floor arena with very long, branched papillae on each lateral border; interior of arena with many pustules in an undivided group, beginning at level of third lateral papillae and extending back to margin of ventral velum. Ventral velum as in *montanum*; median portion with 3 pairs of large papillae.

Median ridge semilunar, margin with 6 short papillae. Buccal roof arena with long lateral papillae; interior completely occupied by pustules, which extend back to dorsal velum. Dorsal velum with 10–12 projections on each side.

REFERRED MATERIAL—BMNH 1978.1526, Mt. Mulu, Fourth Division, Sarawak.

Megophrys nasuta (Schlegel)

Association with adults is based on a developmental series extending from Stages 36 to 42, the terminal member having a pair of long, continuous dermal ridges on the back such as are found in adults. The other species of adult known from low elevations, *M. baluensis,* lacks ridges of that sort. Matsui (1979) assigned 2 tadpoles collected at 1,800 m in a stream on Mt. Kinabalu to *M. baluensis.* He notes that they had nonpigmented venters and based his identification on this character state and their proximity to a spot where 2 adult *baluensis* were caught. In the present sample, the amount of ventral and dorsal spotting varies continuously. Conceivably, larval *baluensis* and *nasuta* may be confounded in the following description, but I have found no means of dividing these tadpoles into two morphological forms.

DESCRIPTION—**External**—Head-body elongate, almost circular in cross section, head-body width .49–.59 of length, depth .78–.86 of width; eyes lateral, visible from below, eyeball .12–.14 of head-body length (Stages 32–41); interorbital .42–.54 of head-body width; nostrils open, rim raised middorsally into short simple or bifid projection. Oral disk terminal, lips expanded into horizontal, dorsally oriented funnel; open funnel as wide as body; anterior margin (i.e., edge of raised lower lip) sinuate, lateral corners pointed; upper lip not as deep (anteroposteriorly) as lower, separated from snout by groove; lips lacking denticles, but set with many short, low ridges (fig. 3); no marginal papillae, but lower lip with low, rounded papillae just inside margin. Beaks thin, both with many long, fine, pointed serrae (fig. 4), upper with median notch. Spiracle sinistral, low on side, tube free of body at tip, snout–spiracle .46–.55 of head-body length. Anal tube median, free of ventral fin. Tail slender, tapering gradually to rounded tip; tail length 1.9–2.4 times head-body length, maximum depth .19–

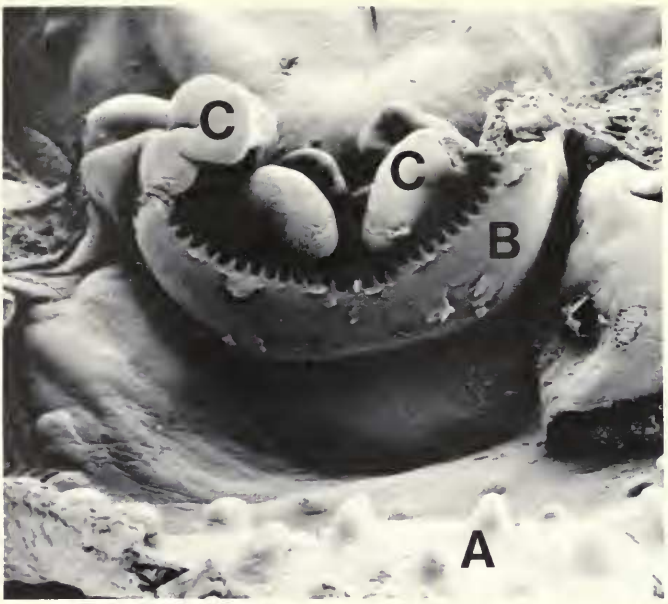

FIG. 4. *Megophrys nasuta.* Lower beak and prelingual palps viewed from anterior (× 72). **A,** Lower lip; **B,** beak; **C,** prelingual palps.

.25 of tail length; caudal muscle deeper than fins except near tip.

Head-body brown above and on sides, ventrally usually spotted with brown; caudal muscle brown, often with a dark, wavy dorsal margin; dorsal fin dusky; ventral fin usually without pigment in proximal two-thirds, dusky near tip.

Head-body lengths (mm): 9.8–11.7 (Stage 36), 12.1 (Stage 39), 12.5 (Stage 41). Total length to 42.2 mm (Stage 41).

Internal Buccopharyngeal (based on FMNH 77508, Stage 36, and FMNH 139503, Stage 34; latter examined by means of SEM)—Prelingual area of floor deep dorsoventrally, with curved, horizontal, slightly raised platform on each side; platform supporting 4 palps or flaps (fig. 5); anteromedial palp curving forward and upward, almost reaching beak; a second palp, concave forward, arising from near posteromedial edge of platform and projecting mesad; a thick, curved flap projecting forward from anterolateral corner of platform; a transverse, smooth-edged ridge between the platforms, curling forward. Tongue anlage indistinct; no lingual papillae. A deep transverse groove behind prelingual area extended by oblique lateral arms backward to just before lateral corners of buccal pockets; a long flange projecting mesad from lateral wall of groove just posterior to beginning of lateral arms; median wall of lateral arm with 4 or 5 pustules; a shallower groove originating at anterolateral angle of main groove, curving around prelingual platform and lateral corner of beak. Buccal floor arena defined laterally by a thick, slightly curved ridge; a long shallow central groove; 1–3 pustules just mesad from lateral ridge. Buccal pocket narrow, curved, transverse; medial to pocket and just behind lateral ridge of buccal floor arena a transverse flap with 3 apical points. Ventral velum without evident spicules; velum much narrowed laterally exposing 2 lateral filter chambers; a weak median notch; margin smooth, without papillae or filaments, secretory pits present. Glottis behind velum. Branchial baskets large; 3 gill chambers on each side, oriented transversely; filters with tertiary folds; filter canals narrow.

Prenarial area of roof (fig. 6) with deep median, U-shaped ridge with ends of arms almost touching beak; a thin, slightly oblique ridge lateral to arm of U; 3 small pustules in transverse row behind lateral ridge; a smooth median knob behind U. Nares transverse, narrow, widely separated; narial walls raised, anterior with 2 or 3 smooth knobs on anterior face; posterior wall with tall, triangular papilla. Postnarial area with shallow groove behind each naris. Lateral ridge papilla triangular, projecting mesad. Median ridge a tall, thick struc-

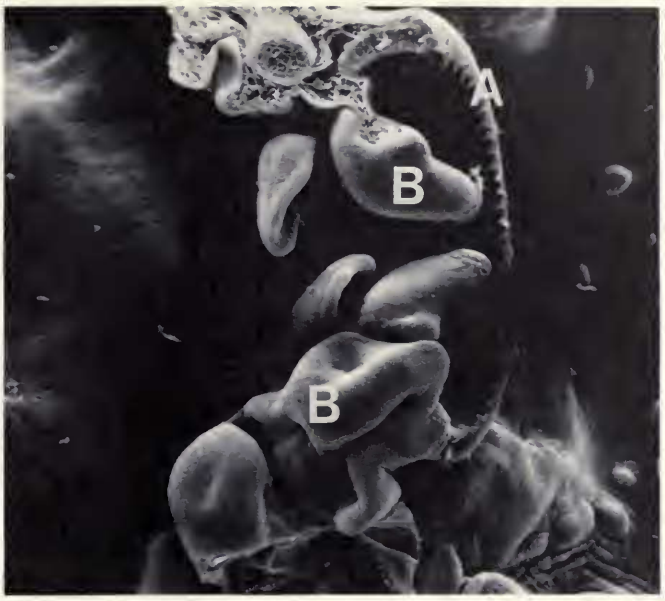

FIG. 5. *Megophrys nasuta.* Prelingual palps, dorsal view (× 77). **A,** Beak; **B,** prelingual palps.

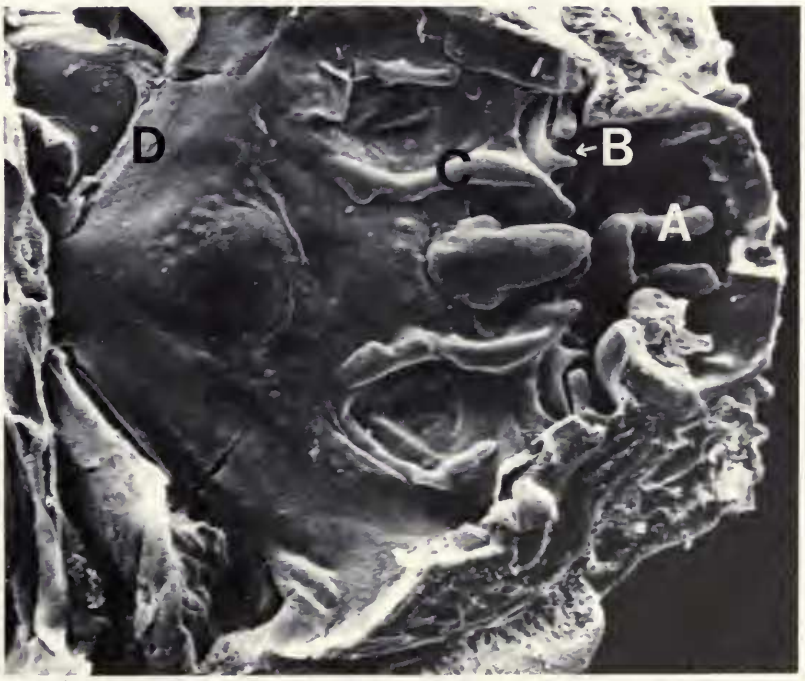

FIG. 6. *Megophrys nasuta.* Roof of buccopharyngeal cavity, ventral view (× 36), anterior to right. **A,** Prenarial ridge; **B,** papilla of posterior narial wall; **C,** ridges of buccal roof arena; **D,** dorsal velum.

TABLE 6. Microhabitat distribution of larval *Megophrys nasuta* in forest streams and their occurrence with tadpoles of other species.

Species	No. of samples					
	Torrent	Riffle	Shingle	Protected side pool	Pothole on bank	Seepage on bank
Leptobrachium gracilis	...	2	...	...	...	...
Leptobrachium montanum	...	1	1	...	...	...
Leptobrachella mjobergi	...	1	2	...	...	...
Amolops phaeomerus	1	1	...	...	...	...
Amolops poecilus	1	1	1	...	...	...
Rana ibanorum	...	...	...	...	1	1
Rana kuhli	...	...	...	1	...	1
Rana signata	...	1	...	...	...	...
Rhacophorus bimaculatus	1	3	4	...	...	...
Without other tadpoles	0	0	1	1	1	0
Total samples	1	3	5	2	1	1

ture jutting forward to median prenarial knob; a deep median recess anterior to base of median ridge. A long, thick, sinuate ridge beginning at median corner of each naris and extending about halfway to dorsal velum; anterior half of ridge flanking median ridge and narrowly separated from it; ridge highest anteriorly. A wide, shallow depression between sinuate ridge and lateral ridge papilla. Area immediately behind median ridge smooth; a V-shaped group of low pustules two-thirds of distance from median ridge to esophagus. Glandular zone with a single row of secretory pits parallel to velar margin; no pits at midline. Dorsal velum smooth.

ECOLOGICAL DISTRIBUTION—Distribution of larval *M. nasuta* is broad, though most samples (8) and individuals (49) were found in areas of moderate current (table 6). They also occur with a variety of other tadpoles. Three samples (4 individuals), omitted from the table because field notes do not adequately define the habitats, were taken with larval *Leptobrachium montanum, Leptobrachella mjobergi, Rana signata* (2 samples), and *Rana kuhli,* species with which they were found in other samples.

REFERRED MATERIAL—FMNH 63520, Bukit Kretam, Kinabatangan District, Sabah; FMNH 77506, Kalabakan, Tawau District, Sabah; FMNH 77507, Matang, First Division, Sarawak; FMNH 77508, 77510, Sungei Entunau, Baleh River, Seventh Division, Sarawak; FMNH 77514, Nanga Putai, Baleh River, Seventh Division, Sarawak; FMNH 139502–3, 148290, 213715–22, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

BUFONIDAE

Tadpoles of three bufonid genera have been found in Borneo, those of *Bufo, Pedostibes,* and *Ansonia.* Larvae of the first two are generalized, having characteristics associated with the majority of bufonid tadpoles of all continents: simple, undivided, finely serrated beaks; marginal papillae confined to the lateral portions of the oral disk; ovoid bodies; and dark, patternless coloration. Larval *Ansonia* are more specialized or divergent, having enlarged oral disks, marginal papillae continuous across the lower lip, and a divided upper beak. Some even have a distinct color pattern.

Larvae have been reported for two other bufonid genera occurring in Borneo, *Cacophryne* and *Pelophryne,* but only from other parts of their geographic ranges. Larval *Pelophryne,* with a large yolk mass even in premetamorphic stages, appear well on the way toward direct development. Larval *Cacophryne* are like most bufonid tadpoles, except that the lower lip has an uninterrupted row of marginal papillae.

The buccopharyngeal cavities in the genera examined, *Bufo* (figs. 9–10), *Pedostibes* (figs. 12–13), and *Ansonia* have relatively few elaborated projections. Most have 6 or fewer short papillae on each side of the buccal floor arena, no papillae on the narial walls, and a smooth though sinuate ventral velum. The interiors of the buccal floor and roof arenas have pustules in larval *Bufo* and *Pedostibes,* as in most Bornean tadpoles, but are smooth in larval *Ansonia.* Tadpoles of *Ansonia* have another distinctive character, a long, conical or triangular, median projection from the buccal roof just anterior to the level of the nares. The

median ridge is at least as tall as wide in all specimens dissected.

Ansonia

Four distinct larval forms have been collected in Borneo. Only one, that of *A. longidigita,* can be assigned to species with reasonable assurance. Three of the forms are very small (head-body < 6 mm), and the fourth, slightly larger (up to 10 mm).

Larval *A. longidigita* is the least modified in general shape from the basic bufonid pattern, having the least flattened body and maximum body width well behind the eyes. The other three are more flattened and have a teardrop shape, with the maximum width at the level of the eyes or even farther forward. The streamlined forms were caught in moderate to strong currents (see below), whereas the many samples of *longidigita* came from areas of weak current (table 7).

Other differences between the streamlined forms and *longidigita,* while confirming the more/less divergent pattern, are not easily related to the microhabitat differences. In *longidigita* the halves of the divided upper beak are narrowly separated, and the margins of the beaks are finely serrated; in the other three, the halves of the beak are widely separated and the margins of the beaks are smooth. The last character state is not found in any other Bornean tadpoles. I was able to dissect the buccopharynx of two of the streamlined forms, and both have the interiors of the buccal roof and floor arenas smooth. In this respect they resemble the torrent-adapted larvae of *Amolops,* most of which also have divided upper beaks.

TABLE 7. Microhabitat distribution of larval *Ansonia longidigita* in forest streams and their occurrence with tadpoles of other species.

Species	No. of samples	
	Leaf drift	Protected side pool
Bufo divergens	...	1
Pedostibes hosei	5	2
Rana blythi	9	4
Rana chalconota	...	2
Rana ibanorum	...	2
Rana signata	8	3
Rhacophorus gauni	1	...
Rhacophorus sp.	1	...
Without other tadpoles	0	0
Total samples	9	5

Ansonia albomaculata Inger

Assignment of these larvae is tentative. The original identification (Inger, 1960b) was based on their small size, which corresponds to the small size of adult *albomaculata,* and on their occurrence at a site where adults were also caught. Subsequently, we collected another tadpole of this form at a second locality where adults of *albomaculata* and adults and larvae of *longidigita* (see below) were also found. Two additional small samples from 885–915 m on Mt. Kinabalu appear to be the same species. Adults of *A. albomaculata* have not yet been reported from higher than 518 m (Inger, 1966). As the most advanced larva is in Stage 38, none is sufficiently mature to have adult features of limbs or coloration that might verify the identification.

DESCRIPTION—**External**—Head-body oval, broadly rounded at snout; maximum width at eyes, .66–.71 of head-body length; body flattened below, depth .59 of head-body width; eyes dorsal, pointing outward, eyeball .12 of head-body length (Stage 36); nostrils open, internarial equal to interorbital and to distance from tip of snout. Oral disk ventral, width .82–.90 of head-body width; both lips expanded; upper lip separated from snout by groove; single row of short fringing papillae continuous across lower lip and on lateral corners of upper; no inframarginal labial papillae; denticles II/III, all rows subequal, widely separated from beaks; beaks black at margins, smooth, upper divided with gap slightly longer than length of one-half. Spiracle sinistral, low on side, tube attached to body wall, snout–spiracle .75 of head-body length. Anal tube median, widely separated from ventral fin. Tail slender, margins straight, tapering only near end to rounded tip; tail length 1.5–1.7 times head-body length, maximum depth .24 of tail length; caudal muscle deeper than fins until distal fourth; origin of dorsal fin just behind end of body, dorsal deeper than ventral except near tip; origin of ventral fin well behind that of dorsal. No glands or lateral line pores visible.

Head-body with well-defined light and dark areas, the latter more extensive; a light median strip on snout ending at interorbital; an interrupted transverse light area across snout before eyes; light vertical bar on side between eye and end of body; ventrally head-body without pigment; caudal muscle dark except midventrally; dorsal fin with dark marginal and basal strips in distal third; ventral fin without pigment.

Head-body lengths (mm): 3.3 (Stage 26), 5.1

(Stage 34), 4.8 (Stage 36). Total length to 11.8 mm (Stage 36).

ECOLOGICAL DISTRIBUTION—Larval *A. albomaculata* is confined to areas of moderate to strong current. Two samples were collected in torrents at low elevations (<300 m). One was caught with larval *Amolops cavitympanum* and *Amolops phaeomerus,* and the other, with larval *Amolops poecilus.* Two samples came from Mt. Kinabalu, 1 from a riffle with larval *Staurois* sp. and *Leptobrachella* at 885 m and 1 from a swift, rocky stream with larval *Leptobrachium montanum* and *Ansonia* sp. at 915 m.

REFERRED MATERIAL—FMNH 130907–8, Sungei Kepungit, Mt. Kinabalu, Sabah; FMNH 83019, Long Seniai, Akah River, Fourth Division, Sarawak; FMNH 167993, Sungei Pesu, Tubau district, Fourth Division, Sarawak; FMNH 213714, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Ansonia longidigita Inger

Assignment of these larvae to *A. longidigita* is based on relative lengths of the first 2 fingers and webbing of the outer toes in Stages 41 to 42. The first finger is only slightly shorter than the second, and the third and fifth toes have less than 2 phalanges free of webbing; *longidigita* is the only species of *Ansonia* known from low elevations in Borneo having this combination of characters (Inger, 1966). Calling males and gravid females of *A. longidigita* were collected along the same small streams in which we caught larvae at Nanga Tekalit.

DESCRIPTION—**External**—Head-body oval, broadly rounded at snout; maximum width behind eyes, .60–.68 of head-body length; body flattened below, depth .62–.73 of head-body width; eyes dorsolateral, pointing outward and upward, eyeball .14–.16 of head-body length (Stages 29–41); nostril open, rim not raised; internarial usually smaller than interorbital and always shorter than distance to tip of snout. Oral disk ventral, width .82–.94 of head-body width; upper lip separated from snout by deep groove; lips slightly expanded; a single row of short marginal papillae continuous across lower lip and on lateral fourth of upper; a short inframarginal row of rounded papillae at lateral corners of both lips; denticles II/III, rows subequal; beaks narrowly edged with black, finely serrated, upper narrowly divided, with gap much less than length of one-half. Spiracle sinistral, low on side, tube attached to body wall, snout–spiracle .68–.78 of head-body length. Anal tube median, free of ventral fin. Tail lanceolate, margins weakly convex, tapering gradually to narrow, rounded tip; tail length 1.4–1.6 times head-body length, maximum depth .26–.30 of tail length; caudal muscle deeper than fins until midlength; origin of dorsal fin just behind body, deeper than ventral fin except near tip; origin of ventral fin just before end of anal tube. No glands or lateral line pores visible.

Head-body in Stage 25 light, with dark cruciform mark dorsally, extended onto caudal muscle; dark spot behind and below eye; dark streak low on side of head from snout to postorbital spot; a dark stripe on side of caudal muscle. Dark areas expand as tadpoles mature.

Head-body lengths (mm): 4.1–4.8 (Stages 28–29), 5.0–5.7 (Stages 34–37), 5.5–5.7 (Stages 38–42). Total length to 14.8 mm (Stage 42).

Each denticle has a well-marked depression near the end of the shaft on the aboral surface (fig. 7). The shaft is margined by 13–17 short, wide cusps, each of which has a buttress-like support.

Internal Buccopharyngeal (based on FMNH 213712, Stage 39, and SEM examination of FMNH 213707, Stage 36)—Both specimens were damaged in dissection, obscuring many details of structure.

Ventral velum without spicules, 2 short, wide projections laterally; no median notch. No glottis. Branchial baskets large, extending far beyond ventral velum, combined areas exceeding that of buccal floor.

Prenarial area of roof with smooth, low, transverse shelf just inside beak; a single, long, median papilla just before line connecting nares. Nares long, oblique, narrowly separated; narial walls low, thin, smooth. Postnarial area with 2 small pustules. Lateral ridge papilla behind lateral corner of naris, behind level of median ridge; bifid at tip; not as tall as prenarial papilla. Median ridge taller than wide.

ECOLOGICAL DISTRIBUTION—Larval *A. longidigita* is limited to areas of slow current in small forest streams (table 7). Its co-occurrence with larval *Pedostibes hosei, Rana blythi,* and *R. signata* is striking. In addition to the samples tabulated, a single tadpole was discovered in a water-filled hole of a fallen tree lying across a stream. Presumably the tadpole got into the hole during a period of high water and was stranded.

REFERRED MATERIAL—FMNH 77526, Nanga Putai, Baleh River, Seventh Division, Sarawak; FMNH 146281, 213701–13, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

FIG. 7. *Ansonia longidigita.* Denticles of inner undivided rows of upper lip (× 2,100). One denticle dislodged, with oral surface exposed and base at left.

Ansonia minuta Inger

Assignment of these young larvae (Stages 25–27) to *A. minuta* was based upon the occurrence of adults of that species where the larvae were collected and on their small size (Inger, 1960b). No additional specimens have been obtained and the identification remains uncertain.

DESCRIPTION—**External**—Head-body teardrop-shaped, snout very broadly rounded, maximum width anterior to center of eyes, .65–.71 of head-body length; body flattened below, depth .43–.59 of head-body width; eyes dorsal, pointing outward, eyeball .08–.11 of head-body length (Stages 25–27); nostril open, rim not raised, internarial greater than interorbital and less than distance to tip of snout. Oral disk ventral, width .89–1.0 of head-body width; upper lip separated from snout by groove; both lips expanded; a single row of short marginal papillae continuous across lower lip and on corners of upper lip; a row of low, widely spaced inframarginal papillae on lower lip except at corners; denticles II/III, well separated from beaks, rows subequal; beaks margined with black, smooth, upper divided with gap 2–3 times length of one-half. Spiracle sinistral, low on side, tube attached to body wall, snout–spiracle .67–.75 of head-body length. Anal tube median, widely separated from ventral fin. Tail slender, margins straight, tapering slightly to rounded tip; tail length 1.6–2.0 times head-body length, maximum depth .17–.22 of tail length; caudal muscle deeper than either fin until distal third; origin of dorsal fin well behind body; origin of ventral fin behind that of dorsal. No glands or lateral line pores visible.

Head-body dark brown above and on sides, without pigment below; caudal muscle dark; dorsal fin dusky throughout except for clear longitudinal streak in distal third; ventral fin colorless except for dark marginal streak near tip.

Head-body lengths 5.8–6.0 mm (Stages 25–27).

Internal Buccopharyngeal (based on FMNH 77521, Stage 26)—Prelingual area of floor posterolaterally with 2 flaps on each side, flaps higher than wide; posterior flap with 3 pointed, subequal projections; anterior one with a long central projection flanked by subsidiary ones. Tongue anlage indistinct; no lingual papillae. Buccal floor arena

with 3–4 short, simple papillae laterally; 3 or 4 pustules or low papillae in posterolateral corner of arena; otherwise arena smooth. Buccal pockets curved, narrow, slightly oblique. Ventral velum without spicules; margin sinuate, no median notch; a single, long, pointed projection far laterally; no secretory pits visible. No glottis. Three gill chambers on each side; filter folds relatively simple, filter canals open.

Prenarial area of roof with a single, median, conical papilla slightly anterior to level of median corners of nares. Nares long, narrow, oblique, gap between them less than half length of one; narial walls low, smooth. Postnarial area with 2 papillae on each side behind lateral third of narial wall; papillae equidistant between median ridge and lateral corners of nares; median papilla stubby with very small pustules, lateral one pointed. Median ridge taller than wide, apex truncate. Buccal roof arena poorly defined; no papillae or pustules. Glandular zone not evident.

The lateral postnarial papilla may be the lateral ridge papilla, which was not otherwise identified.

ECOLOGICAL DISTRIBUTION—Information is limited. Tadpoles of both samples were found clinging to bare rock in strong current. Larvae of *Amolops* (*jerboa*?) were collected with both samples.

REFERRED MATERIAL—FMNH 77521–2, Matang, First Division, Sarawak.

Ansonia sp.

Assignment of these tadpoles, collected on Mt. Kinabalu between 580 and 1,065 m, to a species of *Ansonia* is not possible, although the generic position is certain. A premetamorphic larva (Stage 40) has a short first finger, spatulate tips on the outer fingers, and extensive webbing—a set of character states matched only in *A. hanitschi* and *A. platysoma,* both of which occur in the Kinabalu area. But this geographic correspondence seems to be confounded by the large size of these tadpoles, which have head-body lengths of 8.4–11.2 mm (Stages 28–31). If there is any correlation between size of larva and size of adult in this genus, we would expect the parents of these larvae to be at least the size of adult *A. longidigita* (males to 50 mm, females to 65 mm), which has much smaller larvae (see above). Adults of *hanitschi* and *platysoma* are not known to exceed 32 and 25 mm, respectively (Inger, 1966). Matsui (1979, figs. 12–13) collected 2 tadpoles of this form at 1,260 m on Kinabalu and expressed similar doubts about specific identification.

TABLE 8. Microhabitat distribution of larval *Ansonia* sp. in streams and their occurrence with tadpoles of other species in streams on Mt. Kinabalu.

Species	No. of samples		
	Torrent	Riffle	Open pool
Leptobrachella sp.	...	1	...
Leptobrachium gracilis	...	2	...
Leptobrachium montanum	...	1	...
Megophrys nasuta	...	1	...
Ansonia albomaculata	...	1	...
Amolops sp. E	...	...	1
Amolops sp. F	...	2	1
Rhacophorus bimaculatus	...	1	...
Rhacophorus sp.	...	2	...
Without other larvae	2	0	0
Total samples	2	3	1

DESCRIPTION—**External**—Head-body teardrop-shaped, broadly rounded at snout; maximum width at level of nostrils or slightly anterior to that, width .58–.62 of head-body length; body flattened below, depth .56–.59 of head-body width; eyes dorsal, pointing outward, eyeball .06–.09 of head-body length (Stages 28–36); nostrils open, rim not raised, internarial subequal to interorbital and less than two-thirds distance from tip of snout. Oral disk ventral, width .88–.96 of head-body width; upper lip separated from snout by groove; both lips expanded, lower with wide area between denticles and margin, upper with wide space between beak and denticles; short marginal papillae continuous across lower lip, absent on upper; a double row of low, rounded, inframarginal papillae on lower lip; denticles II/III, upper rows much longer than and circling around ends of lower rows; beaks black, smooth, upper divided, with each half less than .5 of gap between them. Spiracle sinistral, low on side, tube attached to body wall, snout–spiracle .74–.78 of head-body length. Anal tube median, free of fin. Tail slender, margins straight, tapering in distal third to sharp point; tail length 1.7–1.8 times head-body length, maximum depth .18–.21 of tail length; caudal muscle much deeper than either fin until distal third; origin of dorsal fin after proximal fifth of tail, not as deep as ventral fin; origin of ventral fin just behind end of anal tube, in advance of origin of dorsal. No glands or lateral line pores visible.

Head-body dark brown without pattern dorsally

and laterally, without pigment below; caudal muscle dark except midventrally near base; dorsal fin dark throughout, ventral fin only in distal half.

Head-body lengths (mm): 8.3 (Stage 28), 9.2–11.2 (Stage 31), 9.7–9.8 (Stages 34–36), 10.5–10.6 (Stage 40). Total length to 30.8 mm (Stage 31).

Internal Buccopharyngeal (based on FMNH 130911, Stage 36)—Prelingual area of floor with 1 large flap on each side posterolaterally; flap taller than wide, distal half divided irregularly into 2 major and several minor jagged branches; space between flaps greater than basal width of one. Tongue anlage indistinct; 4 short, conical lingual papillae. Buccal floor arena triangular, apex forward; lateral boundary a faint, low ridge with 3–5 short, pointed papillae in posterolateral corners; no other papillae or pustules. No other projections from buccal floor. Buccal pockets narrow, slightly curved and oblique. Ventral velum without spicules, margins sinuate, without marginal projections; secretory pits on medial part of margin. No glottis. Three gill chambers; filter rows without tertiary folds; filter canals open.

Prenarial area of roof with a single median, flattened, pustulose projection just before level of nares, projection as high as wide. Nares elongate, narrow, oblique, widely separated; narial walls low, smooth. Lateral ridge papilla long, pustulose, directly posterior to lateral corner of naris. Median ridge narrow, bifurcate, the arms forming wide U. Buccal roof arena smooth. Dorsal velum damaged in dissection.

Ecological Distribution—These unassigned larval *Ansonia* are clearly restricted to microhabitats of moderate to strong currents in which other similarly specialized tadpoles occur (table 8). Two of the samples listed in Table 8 under "riffle" may have come from torrents; the field notes are not clear on this point. The sample listed under "open pool" came from a portion of stream in which pools and riffles alternated; even in the pools, the current was strong. One sample was obtained at 120 m, the remainder, between 580 and 1,100 m.

Referred Material—FMNH 130909, 130911, 212887, Sungei Kepungit, Sabah; FMNH 131248, Sungei Liwagu, Mt. Kinabalu, Sabah; FMNH 140215, 6 km E. of Tuaran, Sabah.

Bufo asper Gravenhorst

Association of these tadpoles with adults of *B. asper* is based upon a developmental series, including metamorphic individuals that have thin webbing beyond the subarticular tubercles (i.e., only 1 phalanx free of webbing). Webbing of this sort is found in only 2 Bornean species of *Bufo, asper* and *juxtasper*. The absence of crossbars on the hind limbs of metamorphosing larvae reinforces the association. Choice between *asper* and *juxtasper* is based on the great abundance of the former and the relative scarcity of the latter at Nanga Tekalit, Sarawak, where the larvae were found.

These larvae are very similar to those of *B. divergens* (see below), except in later stages, when extent of webbing easily distinguishes them. Otherwise, the main difference between these two forms, evident in all stages after 25, is in the size and position of the posteroventral lobe of the liver, which is visible through the skin. In larval *asper* the anteroposterior length of this lobe is more than .25 of head-body length, whereas it is always shorter than that in larval *divergens*. Furthermore, this lobe reaches the midventral line superficial to the gut in larval *asper* only. The two larval types also differ in size (table 9).

It is difficult to explain why we collected so few samples of tadpoles of one of the commonest amphibians in Bornean forests. Any explanation has to consider that (1) *B. asper* was essentially never found away from stream banks, (2) it breeds throughout the year (Inger & Bacon, 1968), (3) clutch sizes are relatively large compared to other species in these forests, and (4) we tried to collect in every stream and streamside microhabitat we could recognize. The most obvious explanation is that the tadpole of *B. asper* has been misidentified, that the very abundant tadpole assigned below to *B. divergens* is actually the larva of *B. asper*. As association of tadpoles with *B. divergens* is based on larvae reared from eggs of known parentage, we can eliminate this explanation. Given the clutch size and continuous reproductive activity of *asper*, larvae should be numerous, which makes accidents of sampling improbable. The most likely explanation is that, despite our attempts to carry out a comprehensive search of riparian microhabitats, we failed to search the appropriate ones often enough.

Description—**External**—Head-body oval, rounded at snout, slightly flattened above, head-body width .59–.67 of length, depth .69–.77 of width; eyes dorsal, not visible from below, eyeball .11–.13 of head-body length (Stages 35–39); interorbital .21–.25 of head-body width; nostrils dorsal, open, rim not raised, much closer to eye

TABLE 9. Comparison of head-body lengths (mm) of larval *Bufo divergens* and *B. asper* from Borneo.

Species	N	Range	Mean	SD
		Stages 26–29		
divergens	20	4.1–5.3	4.68	.318
asper	7	6.0–6.8	6.21	.288
		Stages 30–33		
divergens	7	4.5–6.5	5.50	.584
asper	3	6.5–7.3	6.75	...
		Stages 34–37*		
divergens	10	5.8–7.3	6.58	.402
asper	6	6.5–7.5	7.06	.467
		Stages 38–41†		
divergens	43	6.6–7.4	6.82	.293
asper	8	7.2–7.8	7.55	.244

* $t = 2.76$, $P = .02$.
† $t = 10.8$, $P < .001$.

than to tip of snout; internarial slightly larger than interorbital. Oral disk ventral, subterminal, width .47–.56 of head-body width; short, thick papillae in a single row confined to extreme lateral corners of both lips; denticles II/III, rows subequal; beaks black at margins only, finely serrated, upper without median notch or convexity. Spiracle sinistral, low on side, tube fused to body wall, snout–spiracle .58–.65 of head-body length. Anal tube median, free of ventral fin most of its length. Tail lanceolate, upper margin convex, lower straight, tapering gradually to broadly rounded tip; tail length 1.5–1.6 times head-body length, maximum depth .24–.30 of tail length; origins of fins at end of body; dorsal fin deeper than muscle beyond midlength, deeper than ventral fin except near tip. No glands or lateral line pores visible.

Head-body dusky above and on sides, pigmentless below; caudal muscle dusky at all points; dorsal fin dusky except near tip of tail; ventral fin dusky only along its base.

The denticles are curved sharply toward the mouth at their apices and have sharp, short, triangular cusps on the distal third of the shaft. Denticles of the upper lip have 8–10 cusps, those of the lower lip, 12–16. Some of the denticles have a weak depression on the aboral surface near the apex.

Head-body lengths in Table 9. Total length to 19.3 mm (Stage 36).

Internal Buccopharyngeal (based on FMNH 213734, Stages 36 and 37, latter examined by means of SEM)—Prelingual area of floor with a large flattened flap in each posterolateral corner, flap with concave face forward, with 6–8 short marginal projections; gap between flaps wider than base of one. Tongue anlage indistinct, 4 short lingual papillae. Buccal floor arena with 5–6 simple, pointed papillae in a row on each lateral border; 8–10 low, rounded pustules across posterior border of arena; interior with 6 similar pustules in rear half. Ventral velum without spicules; margin of velum weakly undulant in middle two-thirds; a broad V-shaped lobe set off by 2 deep notches in lateral corners; no visible secretory pits. No glottis. Branchial baskets small, surface about third of area of floor; filter ruffles with tertiary folds; filter canals open.

Prenarial area of roof with short, curved, transverse pustulose ridge. Nares oblique, oval, widely separated; anterior narial wall pustulose, no papilla; posterior narial wall smooth, no papilla. Postnarial area with an oblique row of 3 papillae on each side, middle papilla of each group tallest. Lateral ridge papilla flat, taller than wide, bi- or trifurcate. Median ridge an attenuate triangle taller than wide, height equals that of lateral ridge papilla. Buccal roof arena with 1 papilla in each posterolateral corner; 6 low pustules in interior. Glandular zone narrow. Dorsal velum with 3 low projections in medial third on each side.

ECOLOGICAL DISTRIBUTION—Microhabitat distributional information is limited: 1 sample of 73 tadpoles was collected from a pool of a rocky stream bank with larval *Rana chalconota* and *R. ibanorum*; a second of 3 was obtained in a torrent with larvae of *Rana blythi* and *Amolops cavitympanum*. The association of forms and microhabitat of the second sample are peculiar, and I believe our field labeling has been confused.

REFERRED MATERIAL—FMNH 213734–5, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Bufo divergens Peters

Association of these larvae with *divergens* is firm; a pair of *Bufo divergens* caught in amplexus laid and fertilized eggs in a plastic bag. Tadpoles developing from those eggs agree in all respects with other wild-caught larvae, some of which were reared to metamorphosis.

DESCRIPTION—**External**—Body and tail shape as in larval *B. asper*. Head-body width .61–.74 of head-body length, depth .63–.74 of width; eyeball .11–.13 of head-body length (Stages 39–40); interorbital .20–.25 of head-body width; width of oral disk .43–.50 of head-body width; snout–spi-

FIG. 8. *Bufo divergens.* Denticles of outer row of lower lip, oblique view (× 2,200). Depression on aboral surface at end of shaft.

racle .65–.70 of head-body length; tail length 1.5–1.9 times head-body length, maximum depth .24–.28 of tail length. Position of eyes and nostrils as in larval *asper.* Oral disk as in *asper,* except that upper beak has a weak median convexity. No glands or lateral line pores visible. Head-body brown dorsally and laterally, without pigment ventrally; caudal muscle brown; dorsal fin dusky, ventral fin dusky only along its base.

Denticles are closely packed in rows and sharply curved toward the mouth near the apex. They have a slight concavity on the aboral surface near the tip and 18–20 triangular, pointed cusps (fig. 8).

Head-body lengths in Table 9. Total length to 22.1 mm (Stage 41).

Internal Buccopharyngeal (based on FMNH 213724, Stage 37, and SEM examination of FMNH 147606, Stage 36)—Prelingual area of floor with a large flattened palp in each posterolateral corner, concave face forward, with 8–10 apical projections; gap between flaps slightly greater than basal width of one (fig. 9); a few pustules between flaps and lower beak. Tongue anlage indistinct, 2 short, thick, widely spaced lingual papillae. Buccal floor arena with a diagonal lateral row of 4 simple, pointed papillae; first 2 with confluent bases; 1 shorter papilla lateral to third papilla on each side; an arched row of low pustules across posterior border of arena, curving forward to short, outer papilla; interior of floor arena with about 20 low pustules in posterior half. Ventral velum without spicules; no median notch; margin gently curved with a single, deep undulation far laterally; margin with many secretory pits. No glottis. Branchial baskets moderate, surface about half area of buccal floor; filter ruffles complexly folded; filter canals open.

Prenarial area of roof (fig. 10) with transverse, arched, pustulose ridge in center; 1 lateral pustule well separated from ridge. Nares oblique, oval, gap between them about length of one; anterior narial wall low, with 2 or 3 small pustules in median corner; posterior wall higher, smooth. Postnarial area with an oblique groove on each side behind nares followed by a low ridge supporting 2 spaced papillae, the median one taller; several low pustules scattered between nares and median ridge. Lateral ridge papilla flattened, bifurcate near tip, taller than wide, adpressed tip separated from median ridge by distance greater than height. Median ridge narrowed above base, taller than wide, 2 or 3 marginal pustules (fig. 10). Buccal roof arena without papillae; interior with widely spaced, low pustules. No glandular zone visible. Dorsal velum thick; margin smooth, set with many secretory pits.

ECOLOGICAL DISTRIBUTION—Larval *B. divergens* is confined to portions of small streams where the current is weak or absent (table 10).

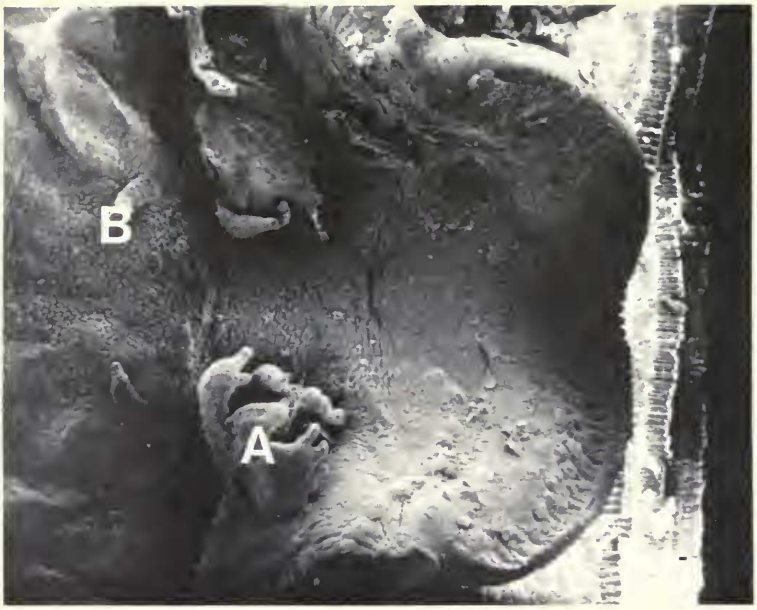

FIG. 9. *Bufo divergens.* Anterior portion of floor of buccal cavity (× 100), anterior to right. **A,** Prelingual palp; **B,** lingual papilla.

REFERRED MATERIAL—FMNH 139525–36, 139538–40, 147607–8, 213723–33, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Bufo sp.

Two samples of tadpoles, collected in nonriparian situations, clearly belong to either *Bufo* or *Pedostibes* because of the restriction of labial papillae to the lateral edges of the oral disk and because of the median position of the anal tube. Although similar to larval *Pedostibes hosei* (see below) in having the inner upper row of denticles divided, these tadpoles differ from those of *Pedostibes* in having a distinct middorsal projection from the rim of the nostril, a bifurcate lateral ridge papilla on the roof of the mouth (rather than one with 5 or 6 projections), dark limbs without light crossbars, and fingers (in advanced stages) resembling those of *Bufo* in shape and relative lengths.

In over-all form and in the details by which they differ from *Pedostibes,* these larvae are similar to those of *B. divergens* and *B. asper.* However, they differ from the last two in the denticular formula they share with *Pedostibes,* in lacking pustules or papillae in the interiors of the buccal floor and roof arenas, and in having the internal nares narrowly separated. Webbing in metamorphic individuals resembles that of *divergens* and is unlike that of *asper.* Finally, the microhabitats from which these unknown tadpoles were taken differ from those recorded for larval *divergens* and *asper.*

Given the characters, internal and external, by which these tadpoles differ from those of *divergens,* it is highly likely that they are larvae of a different species. There remain two possible identifications: (1) *B. quadriporcatus,* adults of which were collected at only one of the localities where the larvae were found, or (2) an as yet undiscovered species of adult. The former alternative seems more likely.

DESCRIPTION—**External**—Head-body oval, rounded at snout, slightly flattened above and below, width .53–.63 of head-body length, depth .60–.62 of head-body width; eyes dorsal in young stages (before 29), dorsolateral in more advanced ones, eyeball diameter visibly increasing with stage of development, .08 in Stage 27, .11 in Stage 40; interorbital .22–.23 of head-body width; nostril open, rim with distinct middorsal projection; nostril slightly closer to tip of snout than to eye; internarial wider than interorbital. Oral disk ventral, subterminal, width .45–.56 of head-body width; short, thick papillae in crowded single row at lateral corners of both lips; denticles I:1 + 1/III, upper rows slightly longer than lower ones; beaks pigmented only near margins, finely serrated, upper with weak median convexity. Spiracle sinistral, low on side, tube attached to body wall, snout–

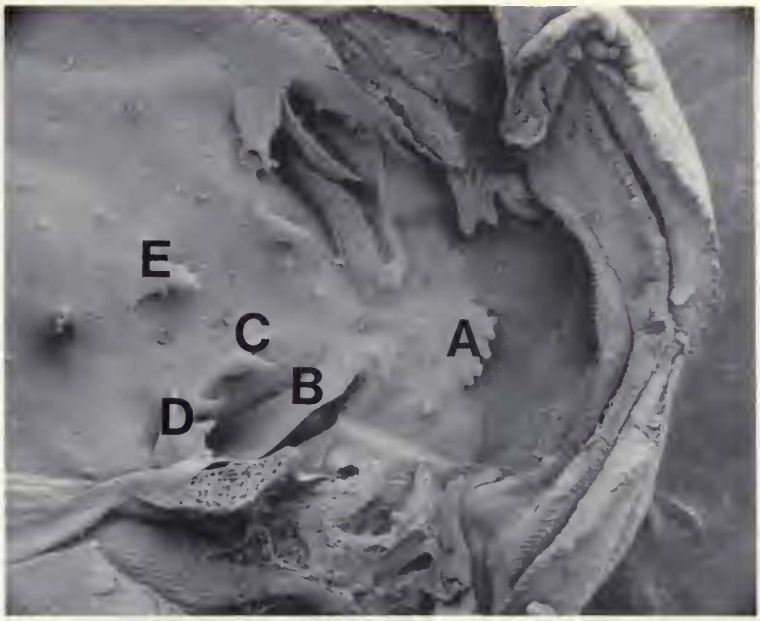

FIG. 10. *Bufo divergens.* Anterior portion of buccal roof (× 50), anterior to right. **A,** Prenarial ridge; **B,** posterior wall of naris; **C,** postnarial papilla; **D,** lateral ridge papilla; **E,** median ridge.

spiracle .70 of head-body length. Anal tube median, attached to ventral fin. Tail narrowly oval, margins weakly convex, tapering to rounded tip; tail length 1.4–1.6 times head-body length; origins of both fins at end of body; dorsal fin deeper than caudal muscle in distal three-fourths. No glands or lateral line pores visible.

Head-body brown above and laterally, without pigment below; caudal muscle and dorsal fin dusky, ventral fin without pigment.

Head-body lengths (mm): 5.7–6.4 (Stages 27–29), 6.1–6.4 (Stages 30–32), 7.1–7.2 (Stages 39–40). Total length to 18.0 mm (Stage 40).

Internal Buccopharyngeal (based on FMNH 195685, Stage 37)—Prelingual area of floor with a large cuplike flap, concave forward, in each pos-

TABLE 10. Microhabitat distribution of larval *Bufo divergens* in forest streams and their occurrence with tadpoles of other species.

	No. of samples			
	Permanent stream			Intermittent stream
Species	Open pool	Protected side pool	Pothole on bank	Pool
Leptobrachium montanum	...	1	...	...
Ansonia longidigita	...	1	...	...
Pedostibes hosei	...	1	...	...
Rana blythi	...	2	...	...
Rana chalconota	...	4	1	...
Rana ibanorum	...	2	2	...
Rana signata	...	1	...	...
Rhacophorus pardalis	...	...	1	...
Microhyla petrigena	...	...	3	...
Without other larvae	1	1	0	1
Total samples	1	5	4	1

FIG. 11. *Pedostibes hosei.* Denticles of upper lip, lateral view (× 2,000). Oral surface to left.

terolateral corner; margins of flaps with 5 or 6 short, thick projections; flaps separated by distance subequal to base of one; no other prelingual projections. Tongue anlage indistinct; 1 short, thick lingual papilla well off midline on right side, none on left. Buccal floor arena pentagonal, narrowed in rear; 5 simple papillae in single row on each lateral border, second and fourth papillae distinctly longer; last papilla separated from corresponding one of other side by gap equal to that between prelingual flaps; no papillae or pustules in interior of arena. No other projections from floor. Ventral velum without spicules; no median notch; median half of margin smooth, gently curved; lateral portion with 2 wide indentations with short projection at each peak; margin with secretory pits. No glottis. Branchial baskets moderate; filter ruffles without tertiary folds; filter canals open.

Prenarial area of roof with flat, smooth shelf behind beak, arching dorsad sharply to general level of roof; short, smooth, transverse ridge medially at rear of prenarial. Nares oblique, large, separated by less than half length of one; anterior narial wall low, smooth except for 1 very low pustule medially; posterior wall thinner, higher, smooth. Postnarial area with oblique groove behind narial wall followed by 3 papillae in an oblique row; middle papilla tallest; no other pustules or papillae in area. Lateral ridge papilla compressed, bifurcate distally. Median ridge triangular, attenuated, smooth; height greater than basal width. Buccal roof arena smooth except for a single papilla on each lateral border. Glandular zone continuous across roof, 3–4 pits deep. Dorsal velum with smooth margin; no secretory pits visible.

ECOLOGICAL DISTRIBUTION—Distribution of these larvae is nonriparian and consequently different from those of other known Bornean bufonid tadpoles. One sample was collected in a small pool of a swampy area and the second reared from eggs found in a water-filled hole of a log at ground level. No other larvae were collected with either sample.

REFERRED MATERIAL—FMNH 151522–7, 195685–6, Labang, Kemena River, Fourth Division, Sarawak; FMNH 195683, Sungei Pesu, Tubau district, Fourth Division, Sarawak.

Pedostibes hosei (Boulenger)

Association with adults is based on a complete developmental series from Stage 25 to metamorphosis. By Stage 42 the outer fingers have spatulate tips and narrow light crossbars typical of juvenile *P. hosei.*

DESCRIPTION—**External**—Head-body oval, slightly flattened above and below, width .60–.66 of head-body length, depth .66–.78 of width; eyes dorsal, eyeball .08–.12 of head-body length (Stages

FIG. 12. *Pedostibes hosei.* Lingual and prelingual areas of buccal floor (× 100). **A,** Prelingual flap; **B,** lingual papilla.

33–39); interorbital .22–.26 of head-body width; nostril open, rim not raised, without projection; internarial slightly narrower than interorbital. Oral disk ventral, subterminal, width .40–.47 of head-body width; lips with short, thick papillae in single row at lateral corners only; denticles I:1+1/III, rows subequal, inner lower row with median indentation but no break; beaks black at margins, very weakly serrated, upper with slight median convexity. Spiracle sinistral, low on side, tube fused to body wall, snout–spiracle .64–.72 of head-body length. Anal tube median, free of ventral fin near its end. Tail lanceolate, both margins weakly convex, tapering to rounded tip; tail length 1.3–1.5 times head-body length, maximum depth .29–.39 of tail length; origins of both fins at end of body, neither as deep as caudal muscle in proximal half. No glands or lateral line pores visible.

Head-body dark brown dorsally and laterally, without pigment ventrally; caudal muscle brown except for narrow pigment-free strip ventrally; dorsal fin with melanophores at origin, otherwise both fins without pigment.

Denticles are closely packed in rows and strongly curved toward the mouth. Each has a slight depression on the aboral surface near the apex, which is somewhat wider than the base of the shaft, and has about 15 short, sharp cusps (fig. 11).

Head-body length (mm): 5.3–6.9 (Stages 26–29), 6.8–7.5 (Stages 30–33), 7.3–8.7 (Stages 34–37), 8.0–8.6 (Stages 38–42). Total length to 19.5 mm (Stage 36).

Internal Buccopharyngeal (based on FMNH 213742, Stages 36–37, latter examined by means of SEM)—Prelingual area of floor with a large cup-like flap, concave forward, in each posterolateral corner; each flap with 10–12 short, thick marginal projections; gap between flaps greater than basal width of one (fig. 12); no other projection from floor in this area. Tongue anlage not distinct, 4 short, thick lingual papillae in a slightly arched, transverse row. Buccal floor arena roughly hexagonal; a double row of papillae in posterior half of each lateral border, 5–6 tall, simple ones in outer row and 5 shorter ones in inner row; 1 tall papilla lateral to rear of double row; interior of arena smooth anteriorly, with about 25 low pustules posteriorly. Buccal pockets narrow, short, oriented transversely; 2 or 3 low pustules anteromedially from median corner of pocket. Ventral velum without spicules; margin gently curved with single deep indentation far laterad; 2 short marginal projections medially on each side followed laterally by 2 more widely spaced ones; dorsal margin and projections with numerous secretory pits. No glottis. Branchial baskets moderate, surface about half area of buccal floor; filter rows with tertiary folds; filter canals open.

Prenarial area of roof with low, short, pustulose ridge posteriorly; no other projections. Nares

FIG. 13. *Pedostibes hosei.* Lateral ridge palp of buccal roof (× 220), anterior to right.

oblique, oval, gap between them about half length of one; anterior narial wall low with 1 short papilla at median corner; posterior wall taller, smooth. Postnarial area with row of 3 papillae on each side parallel to nares, medianmost tallest and pustulose. Lateral ridge papilla compressed, oriented anteroposteriorly, width of base about two-thirds height; margin divided into a long, thick projection at the posterior corner of the apex and into 5 shorter ones on the anterior face and corner (fig. 13); lateral ridge papilla widely separated from median ridge. Median ridge narrowed above base, with pustulose tip about half width of base; height roughly equal to basal width. Buccal roof arena oval, with 4 simple papillae in posterior part of lateral border; posterior border formed by curved row of low pustules extending laterad outside last 1 or 2 lateral papillae; interior with about 20 scattered pustules, 4–6 anterior ones slightly elevated. No glandular zone visible. Dorsal velum with short median gap; each half with 6–8 low projections in medial third, followed by deeper, smooth, thick, lateral section; no secretory pits on velum.

ECOLOGICAL DISTRIBUTION—Larval *P. hosei* is limited to small streams, where it was usually found with several other types of tadpoles (table 11).

REFERRED MATERIAL—FMNH 77520, Kalabakan, Tawau District, Sabah; FMNH 83031, Patah River, Fourth Division, Sarawak; FMNH 157750–1, Labang, Kemena River, Fourth Division, Sarawak; FMNH 77525, Nanga Putai, Baleh River, Seventh Division, Sarawak; FMNH 146318, 213736–45, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Cacophryne borbonica (Tschudi)

Association with adults is based on eggs laid by a female caught in amplexus in Selangor, West Malaysia (Berry, 1972). This larval form has not yet been found in Borneo.

The following description is based mainly on Berry's paper. I have seen the specimens Berry deposited in the British Museum (1974.3130), but they are distorted, making measurement and some observations difficult.

DESCRIPTION—**External**—Head-body oval, slightly depressed; eyes dorsolateral, eyeball .08 of head-body length (Stage 37); interorbital about 2.5 times length of eye; nostrils dorsolateral, pointing anterolaterad, large, oval with a distinct middorsal projection. Oral disk ventral, subterminal; a single row of short marginal papillae continuous across lower lip and on the corners of upper lip; denticles I:1+1/III or 2+2/III; beaks narrowly edged with black, finely serrated. Spiracle sinistral. Anal tube median. Tail with convex margins; tip rounded; fins subequal, origins at end of body. Head-body and caudal muscle black; fins opaque. Berry's drawing shows the underside of the head-body as

TABLE 11. Microhabitat distribution of larval *Pedostibes hosei* in forest streams and their occurrence with tadpoles of other species.

Species	No. of samples			
	Leaf drift	Open pool	Protected side pool	Pothole on bank
Leptobrachium montanum	...	1	1	...
Ansonia longidigita	5	...	2	...
Bufo divergens	...	...	1	...
Rana blythi	5	1	3	...
Rana chalconota	...	...	2	...
Rana ibanorum	...	...	1	...
Rana signata	4	1	...	...
Without other tadpoles	0	0	0	1
Total samples	5	1	3	1

unpigmented. Head-body length 5.5 mm (Stage 37).

Pelophryne brevipes (Peters)

Association of larvae with adults was based on a series reared from ova found in Mindanao. Metamorphosing young have characteristics of *P. brevipes* (Inger, 1960a). Additional clutches of ova from Mindanao have been reared to metamorphosis (Alcala & Brown, 1982). Even if the populations of Mindanao and Borneo ultimately prove to be distinct species, it is very likely that Bornean larvae will be similar to those already reported.

DESCRIPTION—**External**—Head-body ovoid; widest part of body at center of visceral mass; gut with at most 2 coils; maximum width .6 of head-body length; eyes dorsolateral, eyeball .11 of head-body length; nostril anteromesad from eye, not open. Oral disk ventral, subterminal, circular, width .36 of head-body width; lips wide, without lateral indentation, entire margin with very short fringe; 7–26 spaced denticles in single row on upper lip, none on lower; beaks weak, dark at margins, finely serrated. Spiracle not tubular, a simple concave slit near left ventrolateral border, slit just behind level of developing forelimb, snout–spiracle .46 of head-body length. Anal tube median, attached to ventral fin, opening not evident. Tail 1.5 times head-body length, narrow, margins straight, tapering in distal fourth to broadly rounded tip; fins originating at end of body.

Pale straw-colored in preservative, head-body and root of caudal muscle dusted with melanophores; fins without pigment. Stage 45 with a cream band from above axilla to below front of eye.

Alcala & Brown (1982) report that the tail fins of their specimens are highly vascularized. The capillary network is not visible in our specimens.

Head-body lengths 4.0–4.5 mm (Inger, 1960a; Alcala & Brown, 1982).

ECOLOGICAL DISTRIBUTION—Limited to very small pools of water. One sample was recovered from a broken bottle on a forest floor, and 5 were found in leaf axils of *Pandanus* (Alcala & Brown, 1982).

MICROHYLIDAE

Although seven genera of microhylids occur in Borneo (Inger, 1966), tadpoles of only three have been found there: *Chaperina, Microhyla,* and *Kalophrynus.* In addition, we have 1 microhylid tadpole that cannot be assigned to genus with certainty. Larvae of *Kaloula* are known from the continent, but as the Bornean species are not likely to be encountered in rain forest, their larvae would not in any event be included in this publication.

If the two Bornean species of *Calluella* are closely related to the continental forms, their larvae should be similar to those of *C. guttulata*; i.e., they should have an ovoid body, a pointed tail with narrow fins, a terminal mouth, and the spiracle opening near the center of the belly. The larvae of *Gastrophrynoides* and *Metaphrynella* remain unknown, and we have no hints as to their general form, unless the tadpole described below as "Microhylid (genus?)" is the larva of one of them. As both genera utilize tree holes at least part of the time, we expect their larvae to occur in such cavities, which was where 1 sample of the unassigned tadpole was found.

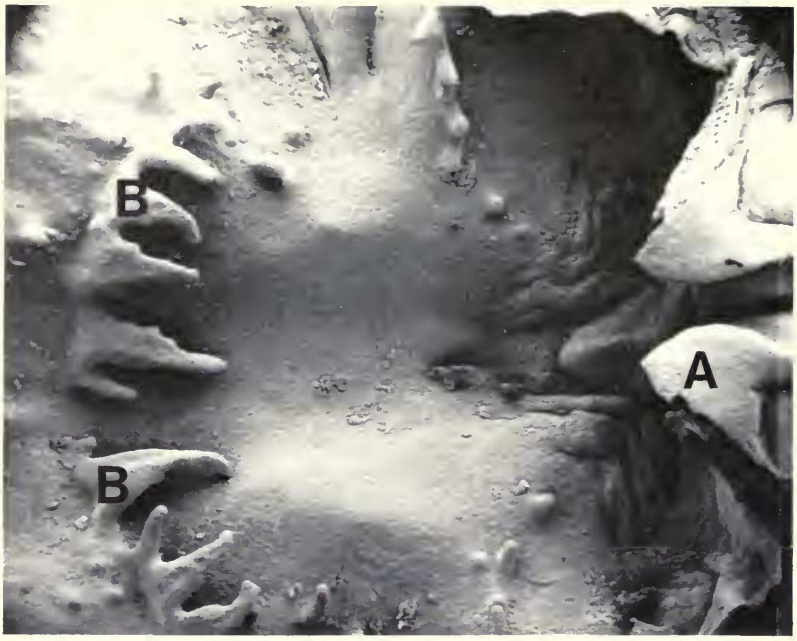

FIG. 14. *Chaperina fusca*. Buccal floor arena (× 53), anterior to right. **A**, Infralabial flange; **B**, papillae of buccal floor arena.

Eight larval forms are described here. Five of them appear to belong to the genus *Microhyla,* giving us more larval forms than known species of adults in Borneo. As adults of this genus are often very small and have cryptic coloration, the existence of undiscovered species seems plausible.

All eight forms are typical microhyline larvae, lacking cornified beaks and denticles and having a median ventral spiracle, the eyes positioned laterally, and nostrils not open until late in development. The buccopharyngeal cavities of the five dissected, representing three of the generic groups, have three distinctive characters noted by Wassersug (1980) in larvae of *Microhyla* from the continent: (1) The glottis is situated far in advance of the rear margin of the velum; (2) the ventral velum is broadly attached medially; and (3) the posteromedial portion of the narial wall is drawn out into a large flap that extends forward under the narial depression.

Chaperina fusca Mocquard

Assignment to species was based on a developmental series culminating in metamorphosing individuals that have the diagnostic dermal spurs at heel and elbow (Inger, 1956). Parker (1934) dissected metamorphic stages and found the strongly curved clavicles and T-shaped terminal phalanges that distinguish *Chaperina* from other Bornean genera.

DESCRIPTION—**External**—Head-body oval, snout truncate; body flattened above, rounded below, maximum width between eyes and end of body, .69–.75 of head-body length, depth .66–.76 of head-body width; eyes lateral, eyeball .09–.12 of head-body length (Stages 27–41); interorbital 3–4 times length of eyeball and almost twice eye–snout distance; nostrils dorsal, not open until Stage 41; internarial less than half of interorbital; nasolacrimal duct conspicuous. Mouth terminal; lips not expanded; upper lip with obtusely pointed, down-turned lateral lobes separated by wide, curved median indentation; lower lip narrow, laterally covered by lobes of upper lip, supporting an infralabial flange (fig. 14) separated from lip by groove and forming part of exterior surface just below center of upper lip. Spiracle median, ventral margin concave, snout–spiracle .74–.83 of head-body length. Anal tube median, in ventral fin, straight, pointing obliquely posteroventrad. Tail weakly convex dorsally, strongly convex below, tapering abruptly near end to rounded tip; tail length 1.9–2.1 times head-body length, maximum depth .33–.34 of tail length; both fins arising at end of body; dorsal fin deeper than caudal muscle

FIG. 15. *Chaperina fusca.* Anterior portion of roof of buccal cavity (× 53), anterior to right. **A,** Lip; **B,** postnarial projection; **C,** median ridge.

in distal half; ventral fin deeper than muscle and dorsal fin. No glands or lateral line pores visible.

Head-body in life black above, lighter below; caudal muscle with black line at dorsal edge, rest of muscle gray, darker distally; fins clear except adjacent to dark line on muscle.

Head-body lengths (mm): 6.7 (Stages 27–29), 6.0–7.2 (Stages 30–31), 6.0–7.1 (Stage 34), 7.2–7.3 (Stage 40). Total length to 21.1 (Stage 40).

Internal Buccopharyngeal (based on FMNH 63529, Stage 34, and SEM examination of FMNH 158019, Stage 34)—Space just inside oral opening almost completely divided horizontally by fleshy infralabial flange; flange free medially and posteriorly and attached anteriorly to the lower lip and posterolaterally to the boundary between roof and floor of mouth; flange narrowest anteromedially, widening abruptly and curving laterally; posterior rim of flange just anterior to level of narial depressions, crossing over middle of tongue anlage. Prelingual area of floor narrow and short, no papillae or pustules. Tongue anlage distinct, length about 1.5 times width; no lingual papillae. Buccal floor arena with shallow, wide, longitudinal depression; posterior border with 10–12 anteriorly directed, pointed papillae in slightly curved row; median pair of papillae longest, outermost shortest, several with confluent bases and pustulose margins (fig. 14); 1 or 2 short papillae just anterior to outermost posterior papillae. Buccal pockets transverse, long, midway between level of tongue anlage and posterior border of buccal floor arena; a row of 4–8 low prepocket papillae from near lateral corner of buccal pocket curving anteromesad toward tongue anlage. Glottis in raised disk just behind buccal floor arena, far in advance of velar margin. Ventral velum attached medially, no spicules; margin sinuous, irregular, curving forward laterally. Branchial baskets very large, combined areas equal to that of buccal floor; gill chambers slightly oblique; filter rows dense, with tertiary folds, overarching canals.

Prenarial area of roof with 2–4 low pustules medially. Nares represented by round depressions separated by slightly less than width of one; medial wall with 3 low pustules; posterior wall with large, forwardly directed flap; flap with margins curled dorsally, margins with pustules or short projections near apex; lateral edge of base extended as thin ridge curving laterally. On extension of ridge a short, triangular papilla (the lateral ridge papilla?); 1 or 2 shorter papillae or pustules anterior to triangular one and lateral to narial depression (fig. 15). Median ridge taller than wide, tip with several short projections. Buccal roof arena with 3–5 short papillae and pustules in posterolateral corner; in 1 individual a row of pustules curving forward and laterally from posterolateral group; scattered, low pustules in interior of buccal roof arena. No glandular zone seen. Dorsal velum with smooth margin.

ECOLOGICAL DISTRIBUTION—Limited to small,

temporary pools of water usually rich in organic matter. One sample was taken in a shallow, silty, leaf-filled depression on a rock outcrop beside a stream. The other 9 samples were found in pools away from streams: holes in logs, a tree hole, and pools on the forest floor. In two instances the water contained enough organic matter to have a foul odor. No tadpoles of other species were found with any of these samples.

REFERRED MATERIAL—FMNH 63517, 63528–30, Bukit Kretam, Sandakan District, Sabah; FMNH 77528, 77532–6, Deramakot, Kinabatangan District, Sabah; BMNH 1914.5.12.19–38, Kuching, First Division, Sarawak; BMNH 1978.95, Mt. Mulu National Park, Fourth Division, Sarawak; FMNH 83029, Patah River, Fourth Division, Sarawak; FMNH 157736–8, Labang, Kemena River, Fourth Division, Sarawak; FMNH 158014–9, Sungei Pesu, Tubau district, Fourth Division, Sarawak; FMNH 146183, 146256, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak; FMNH 96023, headwaters of Baleh River, Seventh Division, Sarawak.

Microhyla

As noted above, five types of larval *Microhyla* have been found in Borneo. One has a tail that tapers gradually from its root to a long, thin filament. The other four have tails with approximately straight margins, abruptly tapering to short, narrow tips. In three of these, the tail has a broad, vertical, black band preceding the narrowed tip. In one of these, the lower lip is expanded, the only one of the five having a funnel mouth. The five larval types may be distinguished by means of the following diagnoses:

A. Tail tapering gradually from root into long, narrow filament; dorsal fin very low over proximal third of tail; both fins dusted with melanophores throughout (in preservative); spiracular flap rounded; lower lip not expanded; head-body length 5.9–6.8 mm (Stages 32–40) ..... *Microhyla borneensis*

B. Tail tapering abruptly in final fourth to short, narrow tip; dorsal fin rising gradually from end of body; fins without melanophores; spiracular flap with crenulate margin; lower lip not expanded; head-body length 3.4 mm (Stage 41) ..... *Microhyla* sp. B

C. Tail shape as in form B; tail with broad dark vertical band crossing both fins just before tip; spiracular flap rounded; lower lip expanded; head-body length 3.8–5.7 mm (Stages 31–40) ..... *Microhyla* sp. C

D. Tail shape as in form B; tail coloration as in form C; spiracular flap fringed; lower lip not expanded; ventral surface of head-body with scattered melanophores; head-body length 2.3–4.1 mm (Stages 26–40) ..... *Microhyla perparva*

E. Tail shape as in form B; tail coloration as in form C; spiracular flap fringed; lower lip not expanded; ventral surface of head-body without melanophores; head-body length 4.0–5.8 mm ..... *Microhyla petrigena*

Forms D and E have been associated with *Microhyla perparva* and *M. petrigena,* respectively, because premetamorphic tadpoles have extremely reduced first fingers as in adults of those species (Inger & Frogner, 1980). Form A was assigned to *M. borneensis* (Inger, 1966) because the first finger in advanced tadpoles, though very short, is distinct from the palm, thus agreeing with adult *borneensis* alone among species of *Microhyla* known from Borneo. Furthermore, adults of *borneensis* were collected at the same locality (Nanga Tekalit) as the larvae. This association, however, while probably correct, is somewhat uncertain because advanced larvae of forms B and C have first fingers of the same shape and proportion as those of form A.

One reason for retaining the assignment of form A to *M. borneensis* rather than B or C has to do with sizes of tadpoles and adults. Forms B and C have approximately the same head-body lengths as larvae of *M. perparva* and *petrigena* (table 12), suggesting that adults of B and C would be about the same size as adults of those species (males 10–16, females 12–18). Form A larvae are 10%–20% larger than larvae of *petrigena,* and adults of *borneensis* (males 18, females 23 mm) (Inger, 1966) are about the same percentage larger than adults of *petrigena.* Smith (1930) and Parker (1934) assigned a quite different developmental series (BMNH 1914.5.12.61–78) from Sarawak to *M. borneensis.* That series differs from form A in having only a short terminal filament on the tail, fins about equal in depth, and the ventral margin of the spiracular tube feebly emarginate. These larvae are also distinctly smaller than form A tadpoles, so that the argument just presented for rejection of B and C as larvae of *borneensis* applies as well to the British Museum series.

Form B, which agrees with larvae of *perparva* and *petrigena* in shape of the lips and tail, might

TABLE 12. Head-body lengths (mm) of larvae of Bornean species of *Microhyla*. Sample size in parentheses.

Larval form	Stages			
	26–29	30–33	34–37	38–41
borneensis	...	5.9–6.1 (3)	6.1–6.2 (2)	6.8 (1)
Form B	...	...	...	3.4 (1)
Form C	...	3.8–4.4 (2)	4.4–4.6 (3)	4.4–4.7 (2)
perparva	2.3–3.5 (4)	...	3.4–4.1 (7)	3.5–4.1 (4)
petrigena	4.0–4.8 (5)	4.8–5.6 (7)	4.7–5.6 (14)	5.7–5.8 (2)

have been considered as conspecific with one of those; the difference in coloration of the tail would be viewed, under that interpretation, as a matter of intraspecific variation. However, the Stage 41 tadpole and all 20 transforming individuals (Stages 42–44) have a clearly projecting first finger, a character state not observed in any adult *perparva* or *petrigena* examined (Inger & Frogner, 1980). The British Museum larvae mentioned above are probably conspecific with form B, agreeing with the latter in all the characters distinguishing them from form A.

Four of the larval forms were collected at Nanga Tekalit, Sarawak—*borneensis,* C, *perparva,* and *petrigena.* The last is ecologically isolated from the others; all 28 samples were collected from potholes of rocky stream banks where no other microhylid tadpoles were caught. The other three forms had overlapping distributions at Nanga Tekalit in microhabitats away from streams (table 13). Morphological differences among these co-occurring forms suggest differences in stratum or mode of feeding. The expanded lower lip of form C indicates that these tadpoles feed at the surface film, if, as seems likely, they behave as do other funnel-mouthed larvae of *Microhyla*; e.g., *M. heymonsi* (Heyer, 1973). Larval *M. perparva* probably feed suspended in midwater in horizontal position as do *M. petrigena* (our observations), which have the same general shape. As vibrations of the tip of the tail are involved in maintaining position in space by other microhylid larvae (Heyer, 1973), as well as *M. petrigena,* the distinctive, attenuated tail of *borneensis* probably signifies behavior different from that of *perparva.*

Microhyla borneensis Parker

Assignment to species is discussed above.

DESCRIPTION—**External**—Head-body almost triangular, snout very wide, flat above, sloping upward from snout to root of tail which is prominently raised; maximum width at eyes, .67–.73 of head-body length, depth .84–.94 of head-body width; eyes lateral, eyeball .15–.17 of head-body length (Stages 32–40); interorbital more than twice length of eyeball, about 1.7 times eye–snout distance; nostrils dorsal, not open until Stages 40–41; internarial less than half of interorbital; nasolacrimal duct usually visible. Mouth terminal, lips not expanded; upper lip a down-turned flap with median notch; lower lip turned inward, supporting U-shaped infralabial flange (see fig. 17). Spiracle midventral, ventral margin forming rounded flap, snout–spiracle .72–.86 of head-body length. Anal tube median, in ventral fin, vertical except for weak posterior angle in last two-fifths. Tail with straight margins, deepest just behind anal tube, tapering gradually to attenuated tip; tail length 2.5–2.8 times head-body length, maximum depth .23–.27 of tail length; origin of dorsal fin well behind body, deeper than muscle only in distal third; origin of ventral fin at end of body, deeper than dorsal fin and caudal muscle throughout. No glands or lateral line pores visible.

Head-body gray except ventrally behind branchial baskets; tail dusky except for proximal fifth of ventral fin.

Head-body lengths 5.9–6.8 mm (table 12). Total length to 22.4 mm.

Internal Buccopharyngeal (based on FMNH 137954, Stage 36, 2 individuals, 1 examined by SEM)—Infralabial flange U-shaped, open to rear, each ramus with a short recurved tip, entire flange attached to lower lip, but demarked by groove. Prelingual area of floor depressed far below level of lip, very short, smooth. Tongue anlage in a central buccal depression that extends back through median part of buccal floor arena and expands to occupy much of the floor arena just anterior to glottis. Buccal floor arena wide, rounded, the lateral and posterior edges of each side defined by 4–5 simple, well-spaced papillae; a single short papilla at posterior boundary immediately in front of glottis. Buccal pockets wide, not perforated,

TABLE 13. Microhabitat distribution of larvae of Bornean species of *Microhyla*. First number in each set from Nanga Tekalit, Sarawak; second number from other localities.

Larval form	Away from streams			Stream-side
	Seepage area	Pool on floor	Hole in log	Pothole on bank
		No. of samples		
borneensis	···	3 + 0	···	···
Form B	···	···	0 + 2	···
Form C	1 + 0	4 + 0	···	···
perparva	···	2 + 1	0 + 1	···
petrigena	···	···	···	28 + 0
		No. of individuals		
borneensis	···	50 + 0	···	···
Form B	···	···	0 + 21	···
Form C	3 + 0	23 + 0	···	···
perparva	···	58 + 8	0 + 5	···
petrigena	···	···	···	1,453 + 0

curving in front of buccal floor arena; median edge formed by ridge defining central buccal depression; anterior margin also ridgelike, with 1 small papilla in center. Glottis in raised area, tipped forward, halfway between end of tongue anlage and rear of ventral velum. Velum deep, broadly attached medially, curving far forward laterally, margin sinuate with 2 widely spaced, short projections; no secretory pits on dorsal surface. Branchial baskets large, extending far behind velum; 3 gill chambers on each side, slightly oblique, length of middle chamber .85 of distance between tongue anlage and rear margin of velum; filter ruffles with tertiary folds, 20–25 rows on wall of middle chamber, filter canals overarched by ruffles (fig. 16).

Prenarial area of roof wide, short, with 1 small median papilla just before level of nares. Nares blind depressions at this stage, rounded, large, gap between them wider than one naris; anterior rim not raised; a large, anteriorly directed, cuplike flap arising from posteromedial corner; median margin of flap with 2 short projections, 1 at middle and 1 near apex; lateral margin of flap extended into low ridge curving laterally on roof behind naris. A small conical papilla just beyond end of ridge; still farther laterad a taller, conical papilla (the lateral ridge papilla?). Median ridge a small, slender, conical papilla. Buccal roof arena with curved lateral row of 5 pustules ending in a conical papilla; posterior boundary of roof arena formed by 2 larger papillae separated by a curved row of 3 pustules; on each side a single pustule midway between large posterior papilla and glandular zone; interior of buccal roof arena with 8 indistinct pustules. An oblique row of 5 or 6 short papillae running posteromesad from anterolateral corner of roof to just outside posterolateral corner of buccal roof arena. Glandular zone consisting of 2 large oval patches narrowly separated in midline. Margin of dorsal velum curved, with 1 short projection.

The buccopharyngeal anatomy is very similar to that of *M. berdmorei* (Wassersug, 1980, fig. 11, mislabeled as *heymonsi*) in the enormous branchial basket and concomitant anterior displacement of the buccal pockets and in the interdigitation of the minor folds of adjacent filter rows (fig. 16). Larval *M. borneensis* may be even more specialized in this direction as they have more filter rows. They lack the infralabial papillae found in *M. berdmorei* (Wassersug, 1980) and further differ from the latter in having a distinct depression surrounding the tongue anlage and occupying the center of the buccal floor arena.

ECOLOGICAL DISTRIBUTION—See Table 13. All 3 samples are from pig wallows, 1 collected with larval *Rana luctuosa* and *Rhacophorus dulitensis*, a second with those 2 plus *Microhyla* form C, and the third without other larvae.

REFERRED MATERIAL—FMNH 83030, below Long Akah, Baram River, Fourth Division, Sarawak; FMNH 137955–6, 139383, 213886, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Microhyla petrigena Inger and Frogner

Assignment to species is based on complete developmental series culminating in metamorphosing young having fingers with the form characteristic of *M. petrigena* (Inger & Frogner, 1980).

DESCRIPTION—**External**—Head-body oval, flattened above, rounded below, snout broadly round-

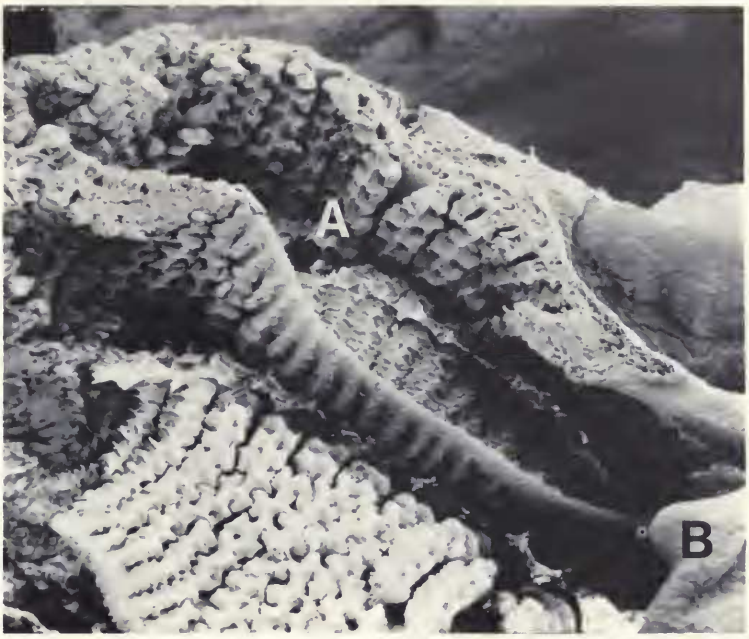

FIG. 16. *Microhyla borneensis.* Portion of left branchial basket (× 119), anterior to right. **A,** Lateral gill chamber; **B,** marginal projection of ventral velum.

ed, maximum body width behind eyes, .61–.73 of head-body length, depth .78–.80 of head-body width; eyes lateral, visible from below, eyeball .10–.15 of head-body length (Stages 27–40); interorbital .50–.60 of head-body width and about twice eye–snout distance; nostrils dorsal, not open until after Stage 39; internarial less than half interorbital, nasolacrimal duct usually visible. Mouth terminal, lips as in larval *M. borneensis.* Spiracle midventral, ventral margin a fringed flap; snout–spiracle .80–.90 of head-body length. Anal tube in ventral fin, running obliquely back to fin margin. Tail with straight margins, tapering abruptly in distal fourth to short, narrow tip; tail length 1.5–2.0 times head-body length, maximum depth .23–.27 of tail length; origin of dorsal fin over end of body, deeper than caudal muscle in distal half; ventral fin beginning at end of body, deeper than muscle beyond proximal fourth, deeper than dorsal fin except near tip. No glands or lateral line pores visible.

Head-body in life black above, whitish below; caudal muscle black; fins without pigment except for broad, vertical black band in third quarter of tail.

Head-body length 4.0–5.8 mm (table 12). Total length to 16.2 mm (Stage 37).

Internal Buccopharyngeal (based on FMNH 211539, Stage 34, FMNH 211546, Stage 37, and SEM examination of FMNH 211539, Stage 34)—Infralabial flange W-shaped, with the outer rami at a 60-degree angle to the median portion which reaches farther forward; entire flange joined to lower lip but separated from latter by groove. Prelingual area deep, underlying infralabial flange, smooth. Tongue anlage triangular, pointed in rear, beneath open middle area of infralabial flange; no lingual papillae. Buccal floor arena a wide V open forward, lateral boundaries formed by 6 or 7 large triangular papillae in an oblique row on each side; anteriormost papilla smallest, situated on medial wall of buccal pocket; posteriormost papilla anterolaterad from glottis; interior of floor arena with single triangular papilla midway between tongue anlage and glottis or a little farther back (fig. 17); rest of arena smooth. Buccal pockets wide, transverse, not perforated, situated far forward, just behind level of tongue anlage; anterior rim with rough, truncate projection in middle and a small pustule near median corner. Glottis on raised disk, tilted forward, about two-thirds of distance from tongue anlage to rear margin of velum. Ventral velum deep, attached medially, laterally curving forward to level of last floor arena papillae; margin

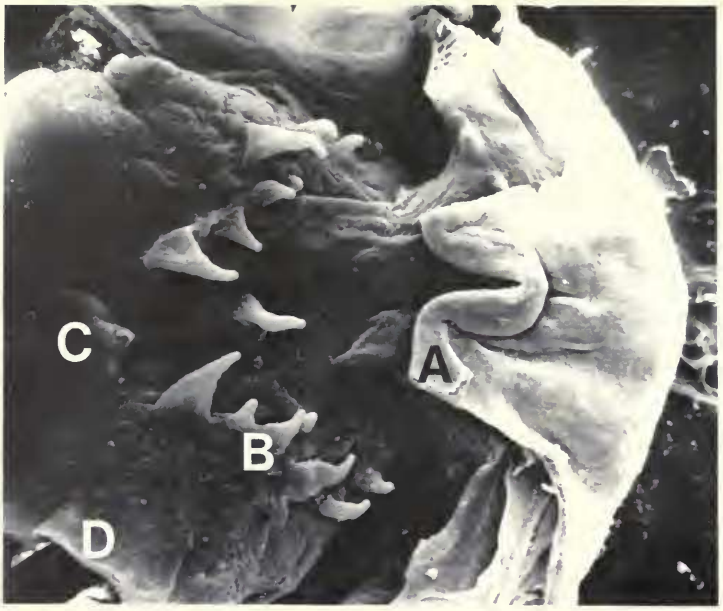

FIG. 17. *Microhyla petrigena.* Floor of buccal cavity (× 53), anterior to right. **A,** Infralabial flange; **B,** papillae of buccal floor arena; **C,** glottal disk; **D,** ventral velum.

sinuate with 2 wide, well-spaced projections; no secretory pits on dorsal surface. Branchial baskets large, extending far behind velum; 3 gill chambers on each side, slightly oblique, length of middle chamber .8 of distance between tongue anlage and rear of velum; filter ruffles without tertiary folds; filter canals open.

Prenarial area of roof wide, short; a single median papilla just anterior to level of nares. Nares round, large, not open, gap between them greater than diameter of one; anterior rim not raised; posteromedian part of rim elevated into large, anteriorly directed, cuplike flap; margins of flap with 2 or 3 weak pustules; lateral margin of flap not drawn out into ridge. A short conical papilla lateral to naris. No median ridge papilla. Buccal roof arena a wide V open forward, bounded on each side by an oblique row of 5–7 low papillae, only the middle one much taller than thick; anteriormost far lateral. Glandular zone consisting of 2 large oval patches narrowly separated in midline. Margin of dorsal velum smooth.

The large branchial baskets and anteriorly located buccal pockets recall larval *borneensis* and *berdmorei.* These larvae, however, have less elaborately folded filter ruffles than larval *borneensis* and differ from both *borneensis* and *berdmorei* in number, size, and distribution of papillae and pustules of the buccal floor and roof arenas.

ECOLOGICAL DISTRIBUTION—Demonstrably among the most restricted of any Bornean tadpole (table 13). Thirteen of the samples came from potholes containing no other kinds of tadpoles. Eleven samples were collected with larval *Rana ibanorum,* 3 with *Bufo divergens,* 2 each with *Rana ingeri* and *Rhacophorus pardalis,* and 1 each with *Rana blythi, Rana chalconota,* and *Polypedates colletti.*

REFERRED MATERIAL—FMNH 137957–70, 211222–7, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Microhyla perparva Inger and Frogner

Assignment of larvae to this species was based upon a developmental series in which a metamorphosing individual (Stage 44) had fingers of size and form typical of *M. perparva* (Inger & Frogner, 1980).

DESCRIPTION—**External**—General form as in *M. petrigena.* Head-body width .67–.76 of head-body length, depth .67–.81 of head-body width; eyeball .15–.19 of head-body length (Stages 25–40); interorbital .46–.58 of head-body width; snout–spiracle .70–.90 of head-body length; tail length 1.7–1.9 times head-body length, maximum depth .20–.25 of tail length. Maximum body width behind

eyes; nostrils as in *petrigena*; lips as in larval *borneensis* and *petrigena*; spiracular tube with fringed flap ventrally; anal tube with short final segment parallel to fin margin; tail as in *petrigena*.

In preservative body dusky in dorsal half; light dusting of melanophores on caudal muscle and on distal third of fins.

Head-body length 2.3–4.1 mm (table 12). Total length to 10.3 mm (Stage 39).

ECOLOGICAL DISTRIBUTION—Limited to small pools removed from streams (table 13). The pool from which 1 sample came also held 2 tadpoles of *Rhacophorus appendiculatus*.

REFERRED MATERIAL—FMNH 167999, Labang, Kemena River, Fourth Division, Sarawak; FMNH 157997, Sungei Pesu, Tubau district, Fourth Division, Sarawak; FMNH 211219–20, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Microhyla sp. B

Difficulties of identification are discussed above.

DESCRIPTION—**External**—Body and tail similar to *M. petrigena*. Head-body width .63 of head-body length; eyeball .15 of head-body length (Stage 41); snout–spiracle .66 of head-body length; tail length 2.2 times head-body length. Maximum body width well behind eyes; upper lip a narrow transverse flap, corners turned slightly upward then down and inward; lower lip separated from snout by groove; infralabial flange V-shaped; ventral margin of spiracle crenulate, without fringes.

Head-body in preservative dusted with melanophores dorsally, laterally, and under chin; caudal muscle evenly dusted with melanophores (black in life?); fins without melanophores.

Head-body length 3.4 mm, total length 11.1 (Stage 41). Snout–vent length 3.7 mm (Stage 43).

The forward-projecting narial flaps (see buccopharyngeal descriptions of *petrigena* and *borneensis*) are visible through the oral opening. The flaps extend forward to the end of the rami of the infralabial flange.

ECOLOGICAL DISTRIBUTION—Appears to be limited to small water-filled containers. Our 2 samples came from holes in logs (table 13) which held no other kinds of larvae. The tadpoles recorded by Smith (1930) and Parker (1934) were found in a *Nepenthes* pitcher.

REFERRED MATERIAL—FMNH 157993, 167995, Sungei Pesu, Tubau district, Fourth Division, Sarawak.

Microhyla sp. C

Identification of this funnel-mouthed tadpole is uncertain (see above).

DESCRIPTION—**External**—Shape of head-body and tail as in *M. petrigena*. Head-body width .56–.59 of head-body length, depth .79–.87 of width; eyeball .14–.16 of head-body length (Stages 31–40); interorbital .58 of head-body width; snout–spiracle .80–.90 of head-body length; tail length 2.1–2.3 of head-body length, maximum depth .19–.22 of tail length. Maximum body width behind eyes; upper lip narrow, turned downward, margin straight; lower lip expanded, horizontal, projecting, free outer margin weakly folded to form poorly defined lobes, supporting infralabial flange; ventral margin of spiracle obtusely pointed or rounded; anal tube bent against curvature of body, then angled sharply and obliquely posteroventrad.

Head-body in preservative heavily dusted with melanophores dorsally, laterally, and under chin; caudal muscle dusted with melanophores throughout; fins without pigment except for broad, dark, vertical band in distal third excluding terminal fifth.

Head-body length to 4.7 mm (table 12), total length to 15.0 mm.

At Stage 38 and beyond, the developing forelimb has a distinctly projecting first finger.

Internal Buccopharyngeal (based on FMNH 137971, Stage 37)—Infralabial flange V-shaped, opening to rear, the end of each ramus bent under itself to form a double V; flange separated from lower lip by groove. Prelingual area of floor with small median papillae. Tongue anlage distinct, pointed at the rear; no lingual papillae. Buccal floor arena smooth anteriorly; 1 short, thick papilla medially in front of glottis; 2 pustules in each posterolateral corner just before level of glottis. Buccal pockets wide, curved, not perforated, anterior margin of pockets .45 of distance from anterior point of buccal floor to margin of velum; anteromedial corner of buccal pocket with 1 papilla slightly larger than median papilla of buccal floor arena. Glottis in raised area, anterior to velum but closer to the latter than to tongue anlage. Ventral velum attached medially; laterally curving forward gently; no projections; no secretory pits visible. Branchial baskets relatively short, strongly oblique.

Prenarial area of roof with thick median papilla, larger than any projecting from floor. Nares oval, not open, gap between them equal to diameter of one; median rim slightly raised, with 1 low papilla;

posterior narial wall with large papilla projecting anteromesad and almost reaching one from other naris; narial papillae almost touching rami of infralabial flange. No median or lateral ridge. Remainder of roof smooth. Glandular zone consisting of single rows of pits posterolaterally, widely separated medially.

The buccal cavity of this form is similar to that of *M. heymonsi* (Wassersug, 1980, fig. 10, mislabeled as *berdmorei*), which also has a funnel mouth. The similarities include: small branchial baskets, posteriorly shifted buccal pockets, and buccal roof and floor arenas with very few papillae. The two forms differ in some details: the infralabial flange in *heymonsi* has a W shape (Wassersug, 1980, fig. 10), whereas in the present species, the rami double under themselves. This Bornean form also lacks the knobs at the rear of the buccal roof and postnarial lateral ridges found in *M. heymonsi.*

ECOLOGICAL DISTRIBUTION—See Table 13. All four forest floor pools yielding samples of this form were pig wallows. Two of these pools also contained larval *Rhacophorus nigropalmatus*; a third contained larval *Microhyla borneensis, Rhacophorus dulitensis,* and *Rana luctuosa.* Larval *Rana ingeri* were collected with this microhylid form in a seepage area.

REFERRED MATERIAL—FMNH 137971–3, 139382, 213885, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Kalophrynus pleurostigma Tschudi

Assignment to this species was based on the relative sizes of the fingers and the presence of a complete procoracoid in transforming young from a developmental series (Inger, 1956). The fourth finger, though shorter than the first, is longer than the terminal phalanx of the third. Larvae apparently identical to these were reared from eggs laid by a female *K. pleurostigma* in a laboratory in Malaya (Berry, 1972).

A second Malayan series differed slightly from the first in size and in shape of the tip of the tail. Berry (1972) suggested that two taxa may be involved. Variation in tail shape comparable to that observed by Berry between samples occurs within a Bornean sample reared from a single clutch of eggs.

DESCRIPTION—**External**—Head-body oval, snout broadly rounded, maximum width between eyes and end of body, .62–.69 of head-body length, depth .79–.86 of width; eyes lateral, eyeball .16–.18 of head-body length (Stages 32–39); interorbital .45–.51 of head-body width, about twice length of eye, much greater than eye–snout distance; nostrils dorsal, not open at Stage 39; internarial about half of interorbital; nasolacrimal duct visible. Mouth terminal; neither lip expanded; upper lip turned down, margin concave; lower lip supporting U-shaped infralabial flange. Spiracle midventral, without free flap, ventral margin concave, snout–spiracle .74–.89 of head-body length. Anal tube median, not open. Tail lanceolate; margins almost straight; tapering to a short, attenuated tip; tail length 1.6–1.9 times head-body length, maximum depth .28–.31 of tail length; origins of both fins at end of body; dorsal deeper than caudal muscle in distal half, not as deep as ventral fin except near tip; ventral fin deeper than muscle in distal two-thirds. No glands or lateral line pores visible. Gut with only a single coil until Stage 36.

Head-body gray in life, in preservative brown above and laterally; ventrally with heavy dusting of melanophores under snout, none behind level of eyes; caudal muscle brownish; dorsal fin dusky, with a clear marginal area widening distally; ventral fin with or without dusting of melanophores.

Head-body lengths (mm): 3.3–3.4 (Stages 31–33), 3.9–4.1 (Stages 35–36), 3.7–3.8 (Stages 39–41), 4.0–4.5 (Stages 43–44). Total lengths to 12.1 (Stage 36).

ECOLOGICAL DISTRIBUTION—Restricted to very shallow, small pools. Two samples were found in a hole in a log, 1 in a small forest floor pool, and 1 in a burrow in a stream bank. No other kind of larvae were found with these samples.

REFERRED MATERIAL—FMNH 63522–26, Bukit Kretam, Sandakan District, Sabah; BMNH 1914.5.12.49–60, Kuching, First Division, Sarawak; FMNH 158005–6, Labang, Kemena River, Fourth Division, Sarawak; FMNH 138057–9, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Microhylid (Genus?)

Identification to family is certain, assignment to genus is not; the midventral spiracle and absence of beaks and denticles are diagnostic of the family. The external nares open only in late stages of development (about Stage 40); the spiracular tube ends at midbody and has a concave ventral margin but no free flap; the intestine has many coils. In metamorphic stages the fingers, other than the first, have very slightly swollen tips, and each has a single rounded but not expanded subarticular tubercle at its base; the palm has 3 flat, oval tuber-

cles; the first finger is less than half the length of the second, which is shorter than the fourth; the toes are partially webbed.

The spiracular tube recalls larval *Chaperina fusca,* but the transforming young lack the dermal spurs at heel and elbow found in *Chaperina.* Furthermore, the smooth buccal floor differentiates these from larval *Chaperina* and *Microhyla.* The last also differ in having a free flap at the end of the spiracular tube. Other features of these tadpoles distinguish them from other larval or juvenile microhylids occurring in Borneo. The short spiracular separates them from *Kaloula,* the multicoiled gut from *Kalophrynus,* and the small subarticular tubercles from juvenile *Metaphrynella.* As these tadpoles were found in tree holes or in plastic containers tied to tree trunks 1–1.2 m above the ground, the fossorial species *Calluella smithi* and *C. brooksi* can be eliminated as possible parents. Only *Gastrophrynoides borneensis,* an adult of which was caught in a tree hole 1.2 m above ground, remains as a potential identification. Agreement with juvenile *G. borneensis* is good in terms of relative length and shape of fingers; however, juvenile *G. borneensis* have no webbing and so differ from these tadpoles.

DESCRIPTION—**External**—Head-body oval, snout rounded, maximum body width well behind eyes, .64–.68 of head-body length, slightly flattened above; eyes lateral, visible from below, eyeball .11–.14 of head-body length (Stages 38–41); interorbital more than twice eye diameter, .43–.52 of head-body width, about 1.5 times eye–snout distance; nostrils dorsal, not open before Stage 40; internarial less than half interorbital; nasolacrimal duct distinct. Mouth terminal, small; upper lip with median half of margin horizontal, lateral portion turning down over lower lip; lower lip not expanded, separated from snout by groove, supporting U-shaped infralabial flange. Spiracle midventral, ventral margin concave, not free; snout–spiracle .71–.75 of head-body length. Anal tube median, in ventral fin. Tail with dorsal margin straight, ventral one convex, tapering gradually to narrow, rounded tip; tail length 1.5 times head-body length; origins of both fins at end of body; dorsal fin not as deep as caudal muscle until distal third; ventral fin deeper than dorsal in proximal half. No glands visible. A dorsolateral row of widely spaced lateral line pores from postorbital area onto caudal muscle.

Head-body dark (black in life?) dorsally and laterally, dusting of melanophores over ventral surface except for clear, circular area anterior to spiracle; fins without melanophores; caudal muscle with scattered melanophores.

Internal Buccopharyngeal (based on FMNH 214701, Stage 38)—Infralabial flange U-shaped with posterior ends of rami bent sharply laterad. Prelingual area short, smooth. Tongue anlage distinct, rounded at rear, length almost twice width; entirely behind infralabial flange; no lingual papillae. Buccal floor arena poorly defined; without projections; a wide central depression running between tongue anlage and glottis. Buccal pockets wide, transverse; immediately behind level of tongue anlage. Glottis in raised area, tilted forward; almost three-fourths of distance from opening of mouth to velar margin. Ventral velum attached medially; lateral margin curving forward to level of glottis; secretory pits not visible. Branchial baskets almost completely exposed behind velum; 3 gill chambers oblique, length of middle one about three-fourths of distance between tongue anlage and rear of velum.

Prenarial area of roof short, wide, smooth. Nares large, circular, not open; gap between them less than diameter of one; anterior narial wall not raised; posterior wall drawn out into large, anteriorly directed flap completely covering narial depression; narial flap obtusely pointed, longer than wide. Lateral to base of narial flap a much smaller similarly shaped flap about one-fourth length and width of narial flap. No median ridge. Buccal roof arena with 2–3 papillae in posterior part of lateral border. No other projections from roof visible. Preservation not adequate for description of glandular zone or dorsal velum.

ECOLOGICAL DISTRIBUTION—Information is limited. One sample was collected in a tree hole 1.2 m above ground, and 4 in water-filled plastic cups being used for rearing mosquitoes at 1–1.2 m above ground. No other tadpoles were found with these samples.

REFERRED MATERIAL—FMNH 213898–900, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

RANIDAE

Rana

This complex, troublesome genus is represented in Borneo by two groups. The first consists of species placed in the "Ranae grunnientes" and "Ranae kuhlianae" sections of the subgenus *Rana*

by Boulenger (1920), with the addition of several species described more recently. The second consists of species belonging to the subgenus *Hylarana.* Within each of these two assemblages, larvae of the various species share many characters.

Larvae of Bornean *Hylarana* usually have moderately robust bodies. All have 3 or 4 subequal rows of denticles on the lower lip and uninterrupted small marginal papillae on the lower lip. A few of the marginal papillae are distinctly larger than the rest in most forms, and 2 have conspicuous patches of glands on the body. The three Bornean forms dissected in this study, *chalconota, luctuosa,* and *signata,* have three features not found in tadpoles of other Bornean ranids: (1) The prelingual area is bounded posterolaterally by a wide, curved flap having its concave surface forward; (2) there is no lateral ridge papilla or flap; and (3) a transverse row of pustules is present immediately in front of the median ridge.

Bornean larvae of the "grunnientes" and "kuhlianae" sections are relatively slender tadpoles. They have narrow, obtusely pointed snouts; relatively narrow oral disks; no more than 2 rows of denticles on the upper lip and 3 rows on the lower lip; the outermost row of denticles on the lower lip no more than two-thirds the length of the others; denticles with 4–8 long cusps; and papillae of the lower lip homogeneous and usually narrowly interrupted medially.

Larval morphology strengthens the definition of *Hylarana* and blurs the distinction between the "grunnientes" and "kuhlianae" sections. Dubois (1981) elevates the latter section to subgeneric rank, with the name *Limnonectes* Fitzinger. As Dubois expands Boulenger's definition (1920) of "kuhlianae" by including *ibanorum,* but not its allied species *blythi* and *macrodon* of the "grunnientes" section, he leaves the status of the last unclear.

To simplify presentation, I will give a complete description for only one larval form for each of the two groups of *Rana* and compare the other larval forms to the appropriate standard—larval *R. blythi* for the "grunnientes" and "kuhlianae" sections and larval *R. chalconota* for *Hylarana.* Buccopharyngeal descriptions will be given for all forms dissected.

Rana blythi Boulenger

Assignment of this larval form to adults of *Rana blythi* is based on a complete developmental series from immature tadpole (i.e., without hind limb buds—Stage 25) to transforming juveniles. The last, though very small (9–11 mm), have diagnostic features of adults: fully webbed toes, narrow flaps of skin on outer and inner toes but not on the fingers, and a dark streak on the side of the snout (Inger, 1966). They look like miniature versions of adult females. We also have one set of 11 larvae reared from eggs stripped and artificially fertilized in the lab using a pair of adults caught in amplexus.

DESCRIPTION—**External** (see Inger, 1966, fig. 33)—Head-body ovoid, obtusely pointed at snout, flattened above, rounded below; maximum width between eye and end of body, .56–.64 of head-body length, depth .62–.79 of width; eyes dorsolateral, not visible from below, eyeball .10–.11 of head-body length (Stages 27–37); interorbital about 1.5 times eye diameter, about two-thirds eye–snout distance; nostrils open, lateral, rim not raised, closer to tip of snout than to eye; internarial equal to interorbital. Oral disk ventral, subterminal, width .22–.32 of head-body width; upper lip with short, thick papillae at corners; lower lip with short, thick papillae in single, staggered row with very narrow gap in center, without inframarginal papillae; denticles I/1+1:II, outermost lower row one-half to two-thirds length of middle row; beaks with narrow black margins, finely serrated (fig. 19), upper beak with wide, weak median convexity. Spiracle sinistral, low on side, tube fused to body wall; snout–spiracle distance .63–.67 of head-body length. Anal tube dextral, attached to ventral fin. Tail lanceolate, both margins weakly convex, tapering gradually to narrow tip; tail length 1.9–2.3 times head-body length, maximum depth .21–.25 of tail length; caudal muscle deeper than either fin in proximal half of tail; origin of dorsal fin just behind end of body, dorsal deeper than ventral fin except near tip. No lateral line pores or glands visible.

Head-body and tail mottled with dark brown (in preservative); wide dark bars radiating from below eye; caudal muscle with wide, zigzag dark band which extends onto fins; both fins spotted along margins.

Denticles, curved slightly toward the mouth, have few cusps (usually no more than 5) whose tips diverge strongly, analogous to extended, spread fingers (fig. 18). The denticles are widely spaced in rows, i.e., the distance between adjacent denticles equals about half the width of a single denticle. They do not appear tightly packed within rows as is the case in tadpoles of *Rana ibanorum* and other related species. The difference is clearly visible at moderate magnification (25×).

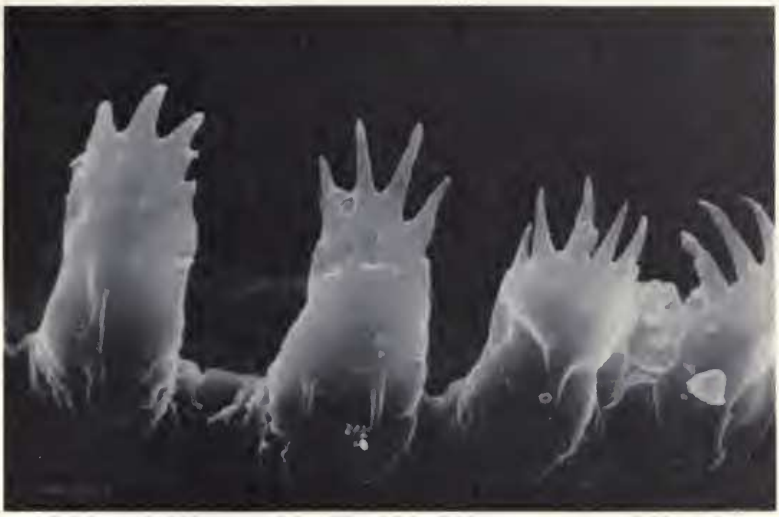

FIG. 18. *Rana blythi.* Denticles of middle row of lower lip, aboral view (× 2,100).

Head-body lengths (mm): 5.4–7.9 (Stages 26–29), 7.0–8.2 (Stages 30–33), 8.5–11.0 (Stages 34–37), 8.9–11.7 (Stages 38–40). Total lengths to 36 mm (Stage 37).

Internal Buccopharyngeal (based on FMNH 96009, Stage 37, and FMNH 213779, Stage 34, latter examined by means of SEM)—Prelingual area of floor bordered posteriorly by 4 palps, a large flattened curved one in each lateral corner and a pair of short, thick palps medially; 2 or 3 low pustules immediately in front of median palps; a short, thick, pustulose papilla in front of each lateral palp; 2 or 3 low pustules just behind beak (fig. 19). Tongue anlage low; 4 slender lingual papillae. Buccal floor arena with 6 or 7 simple papillae in a single row on each lateral border; an additional papilla lateral to penultimate papilla on each side; interior of arena with diamond-shaped group of ca. 50 low pustules, leaving bare triangular area anteriorly on each side; posterior pustules extending onto velum. Buccal pockets oblique, wide; ca. 12 low prepocket pustules. Ventral velum supported by spicules; margin with 2 short, widely separated projections on each side; no median notch; velum without secretory pits on dorsal surface. Glottis completely exposed behind velum. Branchial baskets large, surface about .8 of buccal floor area; 3 gill chambers; filter rows with tertiary folds; filter canals narrow.

Prenarial area of roof of mouth crossed by low, transverse, pustulose ridge; 1 low, thick pustule lateral to ridge. Nares transverse, separated by less than half length of one; anterior narial wall low, several low pustules medially and a short, medially curved papilla rising from its middle third; posterior narial wall valvular, with a short triangular projection at medial corner. Postnarial area with a groove behind each naris; a tall postnarial papilla rising from medial corner of rear wall of postnarial groove. Lateral ridge papilla laterally compressed, oriented anteroposteriorly, height equal to that of postnarial papilla, 4 short projections from margin. Median ridge triangular, wider than high. Buccal roof arena with 6 simple, pointed papillae on each lateral border; entire interior of arena occupied by ca. 100 low, evenly spaced pustules. No evident glandular zone. Dorsal velum with smooth or slightly wavy margin.

ECOLOGICAL DISTRIBUTION—Distribution of larval *R. blythi* is relatively broad within streams, though essentially confined to microhabitats having little or no current. These are also microhabitats used by a variety of tadpoles (table 14). One sample, containing 1 tadpole of *R. blythi,* was omitted from Table 14 because the label "torrent" seems dubious; this sample also included 1 tadpole of *Amolops poecilus.*

REFERRED MATERIAL—FMNH 77552, 77561, Kalabakan, Tawau District, Sabah; FMNH 158020–1, 158023, Sungei Pesu, Tubau district, Fourth Division, Sarawak; FMNH 77581, Nanga Putai, Baleh River, Seventh Division, Sarawak; FMNH 96007–9, headwaters of Baleh River, Seventh Division, Sarawak; FMNH 139548–49, 139551–54, 213749–86, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

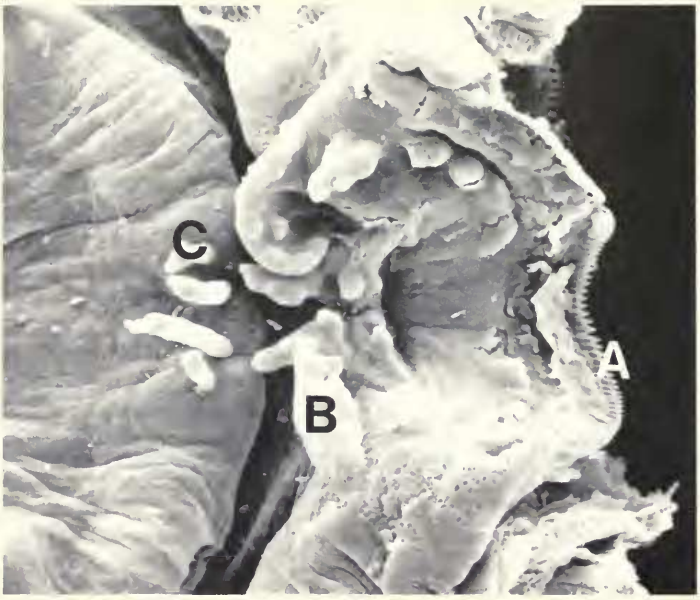

FIG. 19. *Rana blythi.* Anterior portion of floor of buccal cavity (× 100), anterior to right. **A,** Beak; **B,** prelingual palp; **C,** lingual papilla.

Rana finchi Inger

Association of this larval form with adults is based upon agreement in characters of the limbs in advanced stages (39 onward): tips of toes expanded, webbing of outer toes not full to disks. These tadpoles are very similar to those assigned here to *R. palavanensis* and *R. ingeri.* The reduced webbing eliminates the latter from consideration as the parental species. Larval *finchi* differs from larval *palavanensis,* a species (or subspecies) not reported from northeastern Borneo, in having less deep tails (maximum depth less than .22 of tail length as compared to greater than .23).

DESCRIPTION—**External**—Generally similar to larval *R. blythi.* Head-body width .57–.64 of head-body length, depth .68–.72 of width; eyeball .09–.12 of head-body length (Stages 36–40); oral disk width .29–.34 of head-body width; snout–spiracle .59–.67 of head-body length; tail length 1.7–1.8 of head-body length, maximum depth .20–.21 of tail length. Lower lip with narrow median gap in marginal papillae; no inframarginal papillae; denticles I:1+1/1+1:II, outermost lower row about half length of middle row; beaks black along margins, finely serrated, upper without median convexity. Lateral line pores barely discernible above eye.

Head-body dorsally and laterally with indistinct, irregular dark spots; dark vertical bars on side of head, but not radiating from eye; caudal muscle with irregular dark pattern; dorsal fin with vertical dark bars continuous with markings on muscle, pattern becoming irregular distally; ventral fin without pigment in proximal half.

Head-body lengths 7.6–8.2 mm (Stages 36–39). Total lengths to 23.0 mm.

Internal Buccopharyngeal (based on FMNH 63514, Stage 36)—Prelingual area with a flattened palp in posterolateral corner, with 3–4 apical projections, width greater than height; a short, thick papilla anterior to lateral corner of palp; a pair of short papillae medially at posterior edge of prelingual. Tongue anlage indistinct, wider than long; 4 short lingual papillae in transverse row. A deep longitudinal furrow running back behind tongue anlage, branching with arms extending half length of buccal floor arena. Buccal floor arena rectangular, about as wide as long; 7 or 8 long, pointed, simple papillae in a staggered row on each lateral border; about 50 low pustules in interior of arena, covering full width posteriorly, but confined within postlingual furrows anteriorly, leaving wide, smooth area anterolaterally; low pustules in a group spreading from just inside anterior buccal arena papillae laterally across floor anterior to buccal pockets. Buccal pockets wide, transverse, curved; at level of second buccal arena papillae. Ventral velum wide, supported by spicules; no median notch; margin weakly sinuate, without projections; no secretory pits visible at 50×. Glottis behind

TABLE 14. Microhabitat distribution of larval *Rana blythi* in forest streams and their occurrence with tadpoles of other species.

Species	No. of samples				
	Riffles	Leaf drift	Open pool	Protected side pool	Pothole on bank
Leptobrachium montanum	...	...	4	1	...
Leptobrachium nigrops	...	...	...	1	...
Ansonia longidigita	...	9	...	4	...
Bufo divergens	...	...	...	2	...
Pedostibes hosei	...	5	1	3	...
Microhyla petrigena	...	...	...	...	1
Rana chalconota	...	...	1	1	2
Rana ibanorum	...	...	...	9	3
Rana ingeri	...	...	...	...	1
Rana kuhli	...	...	...	1	...
Rana signata	...	8	...	4	...
Rhacophorus gauni	...	1	...	...	...
Amolops poecilus	1	...	...	...	...
Rhacophorus sp.	1	...	...	...	...
Polypedates colletti	...	...	...	1	...
Without other tadpoles	0	0	1	3	1
Total samples	1	9	3	19	5

velum. Branchial baskets largely behind velum; 3 gill chambers on each side, slightly oblique; filter ruffles with tertiary folds; 9 filter rows on median wall of middle chamber; filter canals open.

Prenarial area of roof with a tall, transverse, curved ridge having a fringed margin; ridge about midway between beak and nares; laterally 2 short, conical papillae in extension of curve of ridge. Nares transverse, oval, gap between them about two-thirds length of one; anterior narial wall thick, low, with short, medially curved papilla in its center flanked laterally by 2 low pustules and medially by 3 or 4 larger ones; posterior narial wall thin laterally, with a tall, medially curved papilla near its median corner. Postnarial area with a groove behind each naris; groove bounded posteriorly by a thin ridge bearing a tall papilla at its median corner, papilla tallest projection in roof, pustulose on its lateral margin; no other postnarial papillae. Lateral ridge papilla compressed laterally, taller than wide, apex pustulose. Median ridge triangular, height almost equal to width of base, 3 small pustules at apex. Buccal roof arena rectangular; 5 simple, medially curved papillae on each lateral border; entire interior occupied by about 75 evenly spaced pustules extending behind level of papillae. Glandular zone narrowly interrupted medially, at least 10 pits deep laterally, much narrower medially. Dorsal velum damaged in dissection.

ECOLOGICAL DISTRIBUTION—Larval *finchi* is probably restricted to pools of rain water on the forest floor. One sample was collected in such a pool, as was the male reported carrying tadpoles (Inger, 1966).

REFERRED MATERIAL—FMNH 63514, Bukit Kretam, Sandakan District, Sabah; FMNH 63515, Sapagaya Forest Reserve, Sandakan District, Sabah.

Rana ibanorum Inger

Assignment of these larvae to this species is based on a complete developmental series through metamorphosis. Advanced larvae have fully webbed feet, a relatively short toe, and a flap of skin on the inner margin of the fourth finger, a combination of character states occurring only in *R. ibanorum* among the species living along these Bornean streams (Inger, 1966).

DESCRIPTION—**External**—Generally similar to larval *R. blythi*. Head-body width .61–.71 of head-body length, depth .68–.74 of head-body width; eyeball .11–.13 of head-body length (Stages 27–38); oral disk width .26–.34 of head-body width; snout–spiracle distance .55–.64 of head-body length; tail length 1.8–2.2 times head-body length, maximum depth .21–.25 of tail length. Lower lip with short, thick marginal papillae, gap in papillae at center of lip; 2 or 3 inframarginal papillae wedged between inner rows of denticles at corners of oral disk; denticles I:1+1/1+1:II, outermost lower row two-thirds length of middle row; upper beak with-

FIG. 20. *Rana ibanorum.* Denticles of outer row of lower lip, aboral surface (× 2,600).

out median convexity. Lateral line pores visible in curved row above eye.

Head-body mottled brown dorsally and on sides; no clearly defined bars around eye; caudal muscle mottled; dorsal fin speckled, ventral speckled in distal half.

Head-body lengths (mm): 5.3–8.7 (Stages 26–29), 7.5–8.8 (Stages 30–33), 8.4–9.5 (Stages 34–37), 8.2–10.4 (Stages 34–42). Total length to 36.0 mm (Stage 36).

The denticles are densely crowded within rows. They are curved toward the mouth apically and have 6–10 long, triangular cusps in the apical third of the shaft (fig. 20).

Internal Buccopharyngeal (based on FMNH 96004, Stage 34, FMNH 77580, Stage 37, and FMNH 213857, Stage 35; last two examined by means of SEM)—Prelingual area of floor with a large, transversely oriented flap in each posterolateral corner, flaps with stubby marginal projections, distance between flaps greater than basal width of one; a median pair of short papillae between flaps preceded by a pair of still smaller papillae on each side; a short papilla laterally anterior to flap; a transverse row of 3 or 4 pustules anterior to lateral papilla. Tongue anlage short, wide, poorly defined laterally; 4 cylindrical, subequal lingual papillae in curved transverse row (fig. 21). Buccal floor arena rectangular, almost as wide as long; 10–14 papillae in staggered double row in posterior half of each lateral border, anterior papillae taller, 1 or 2 branched apically; interior of arena with 15–30 low pustules mainly in posterior two-thirds; a band of about 25 pustules forming posterior border of arena and extending onto velum (fig. 21). Buccal pockets curved, slightly oblique; pockets at same level as second or third papillae of buccal floor arena; about 6 small prepocket pustules.Ventral velum with spicules; no median notch; margin with 6 short projections on each side, the median 3 closer together; no secretory pits visible on dorsal surface or margin. Glottis exposed behind velum. Branchial baskets largely exposed behind velum; combined area of baskets subequal to area of buccal floor; 3 gill chambers on each side, oblique, length of middle chamber almost two-thirds length of floor behind prelingual area; filter ruffles with tertiary folds; about 12 filter

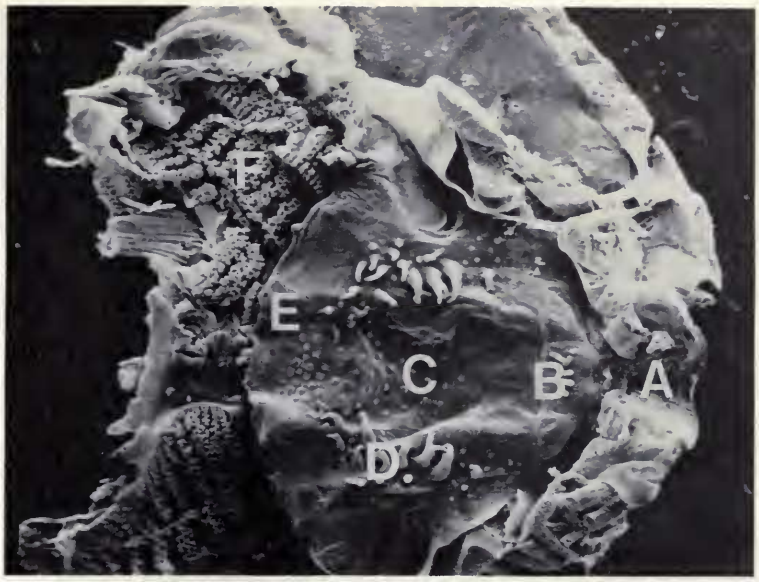

FIG. 21. *Rana ibanorum.* Floor of buccopharyngeal cavity (× 33), anterior to right. **A,** Prelingual area; **B,** lingual papillae; **C,** buccal floor arena; **D,** papillae of buccal floor arena; **E,** ventral velum; **F,** branchial basket.

rows on median wall of middle chamber; filter canals open.

Prenarial area of roof longer than wide; a forwardly arched, transverse ridge with irregular or pustulose margin; 1–3 low papillae or pustules laterally. Nares oval, narrow, transverse, gap between them half length of one; anterior narial wall low, a short medially curved papilla in its middle portion, margin pustulose medially; posterior narial wall same height as anterior, margin smooth. Postnarial area with deep groove parallel to posterior narial wall; a tall, medially curved, pustulose papilla rising from middle of rear edge of groove (fig. 22); a transverse row of 3–4 very short projections just anterior to median ridge; 1 or 2 pustules on each side between transverse row and tall postnarial papilla. Lateral ridge papilla behind lateral corner of naris, flattened, orientation anteroposterior, almost as wide as tall, margin with 5–7 projections (fig. 22). Median ridge low, base 2–4 times height, margin with 2–6 small peaks. Buccal roof arena (fig. 23) oval, 6–8 unbranched papillae on each lateral border; entire interior behind median ridge with about 100 uniformly spaced pustules. Glandular zone continuous. Dorsal velum with 6–8 low projections laterally, smooth medially.

ECOLOGICAL DISTRIBUTION—Larval *R. ibanorum* is almost confined to stream microhabitats of weak or no current, and in these situations it occurs with numerous other kinds of tadpoles (table 15).

REFERRED MATERIAL—FMNH 158022, Sungei Pesu, Tubau district, Fourth Division, Sarawak; FMNH 77580, 77582–3, Nanga Putai, Baleh River, Seventh Division, Sarawak; FMNH 96001–6, 96011, headwaters of Baleh River, Seventh Division, Sarawak; FMNH 139566–8, 148354, 151502, 213831–75, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Rana ingeri Kiew

Assignment of these larvae to *R. ingeri* is based upon a combination of character states in advanced stages encountered only in adults of this species among those occupying the streams in Sarawak where the larvae were collected. Advanced tadpoles (Stages 41–43) have an oval inner but no outer metatarsal tubercle; expanded toe tips; flaps of skin along inner edge of first toe and outer edge of fifth; first finger longer than second; toes fully webbed to tips, but with webbing deeply excised between fourth and fifth. These character states apply to *R. blythi, R. ibanorum, R. kuhli,* and *R. ingeri,* except for the excision of the web, which is found only in *ingeri.*

DESCRIPTION—**External**—Similar to larval *R. blythi.* Head-body width .65–.73 of head-body length, depth .71–.73 of width; eyeball .13 of head-

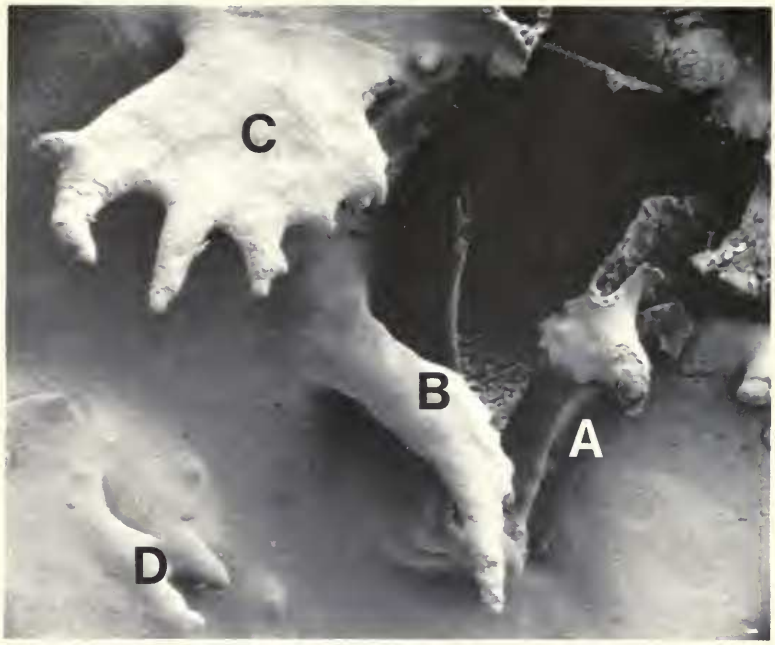

FIG. 22. *Rana ibanorum.* Narial region of buccal roof (× 110), anterior to right. **A,** Anterior narial wall; **B,** postnarial papilla; **C,** lateral ridge palp; **D,** median ridge.

body length (Stages 39–41); width of oral disk .19–.29 of head-body width; snout–spiracle .58–.61 of head-body length; tail length 1.6–2.0 times head-body length, maximum depth .25–.26 of tail length. Lower lip with short papillae in single, crowded row, continuous or with narrow gap in center, no inframarginal papillae; denticles I:1+1/1+1:II, outermost lower row half length of middle row; beaks half pigmented, finely serrated, upper without median convexity. Lateral line pores in double rows around eye and dorsolaterally behind eye to end of body.

Head-body dusky dorsally and laterally, without clear pattern, faint crossbar over end of body; no dark bar below eye; caudal muscle speckled with dark spots on dorsal surface; ventral surface of muscle without pigment; dorsal fin speckled throughout; ventral fin speckled in distal half.

Head-body lengths (mm): 5.8–7.7 (Stages 26–29), 6.5–8.9 (Stages 30–33), 8.5–9.4 (Stages 34–37), 7.5–10.0 (Stages 38–42). Total length to 27.9 (Stage 39).

The denticles are crowded within rows. They have relatively short shafts with 5–7 slender apical cusps curved toward the mouth (fig. 24).

Internal Buccopharyngeal (based on SEM examination of FMNH 213876, Stage 38)—Prelingual area of floor with a pair of thick, branched palps posterolaterally on each side; short, thick papillae anteromesad from palps; a forwardly arched, pustulose transverse ridge immediately in front of papillae; all of these structures in posterior half of prelingual area. Tongue anlage obscure; 4 lingual papillae in transverse row directly behind gap between prelingual palps. Buccal floor arena roughly oval; 7 conical, unbranched papillae in a double row in posterior half of each lateral border; interior of floor arena with about 50 evenly spaced, rounded pustules in a triangular group, apex forward at the level of first lateral papillae, group spreading to cover entire space between posterior corners and extending back onto velum. Buccal pockets oblique, narrow, curved; a few low pustules anterior to pockets. Ventral velum with spicules; no median notch; margin with 4–6 short projections; margin with secretory pits. Glottis damaged in dissection. Branchial baskets largely exposed behind velum; 3 gill chambers on each side, oblique, middle chamber about two-thirds length of buccal floor behind prelingual area; filter ruffles with tertiary folds; more than 9 filter rows on median wall of middle chamber; filter canals canopied.

Prenarial area of roof with notched transverse ridge, closer to level of nares than to beak, flanked on each side by an isolated papilla. Nares oval,

FIG. 23. *Rana ibanorum*. Buccal roof arena (× 55), anterior to right. **A**, Median ridge; **B**, lateral ridge palp; **C**, buccal roof arena; **D**, papilla of buccal roof arena.

transverse, gap between them about half length of one; both narial walls raised, but low; anterior wall with short, medially curved papilla at its center; 2 or 3 pustules on anterior wall medially; posterior wall smooth, median corner drawn out into smooth, triangular projection. Postnarial area with deep groove behind each naris; a tall, medially curved papilla rising near median corner of groove, papilla with 3 pustules on its lateral margin (fig. 25); no other projection in postnarial area. Lateral

TABLE 15. Microhabitat distribution of larval *Rana ibanorum* in forest streams and their occurrence with tadpoles of other species.

Species	No. of samples			
	Shingle	Protected side pool	Pothole on bank	Seepage on bank
Leptobrachium montanum	1	...	...	...
Megophrys nasuta	...	...	1	1
Ansonia longidigita	...	2	...	...
Bufo asper	...	...	1	...
Bufo divergens	...	2	2	...
Pedostibes hosei	...	1	...	...
Rana blythi	...	9	3	...
Rana chalconota	...	8	5	...
Rana ingeri	...	...	3	1
Rana kuhli	...	...	...	2
Rana signata	...	2	...	...
Rhacophorus bimaculatus	1	1	...	...
Polypedates colletti	...	...	1	...
Rhacophorus pardalis	...	...	2	...
Microhyla petrigena	...	...	10	...
Without other tadpoles	0	3	5	0
Total samples	1	15	23	2

FIG. 24. *Rana ingeri.* Denticles of outer row of lower lip, aboral surface (× 2,180).

ridge palp just behind lateral corner of naris, flattened, orientation anteroposterior, 3 short apical projections and 1 on anterior margin; height of palp greater than width. Median ridge a low triangle, much wider than high; margin with short projections (fig. 25). Buccal roof arena rectangular, longer than wide; 5 conical, unbranched papillae in a row along middle two-thirds of lateral border; a shorter papilla lateral to fourth one in row; entire interior of arena occupied by about 50 pustules that decrease in size and increase in density posteriorly. Glandular zone continuous, 4–6 pits deep. Dorsal velum with 5 short, finger-like projections on left side; right side damaged.

ECOLOGICAL DISTRIBUTION—Distribution of larval *R. ingeri* is narrow. Six samples were collected in potholes on stream banks, 1 in a seepage on a stream, and 1 in a nonriparian seepage on the forest floor. Those from potholes were collected with larval *R. blythi* (1 sample), *R. ibanorum* (3), *Polypedates colletti* (2), and *Microhyla petrigena* (2). The sample from the streamside seepage was collected with larval *R. ibanorum* and *R. kuhli,* and the nonriparian sample, with larval *Microhyla* sp. C.

REFERRED MATERIAL—FMNH 77579, Nanga Putai, Baleh River, Seventh Division, Sarawak; FMNH 213876–82, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Rana kuhli Duméril and Bibron

Assignment of these larvae is based on a development series from Stages 25 to 44. The transforming individuals have fully webbed feet with flaps of skin along the edges, lateral fringes on the fingers, no loreal stripe, and no blotches on the throat. This combination of character states is found only in *R. kuhli* among the ranids occurring in Sarawak. Though very similar to larval *R. ingeri,* they differ from those in having inframarginal papillae on the lower lip, in the shape of the denticles, in having larger serrae on the beaks, and in several aspects of the buccopharyngeal cavity.

DESCRIPTION—**External**—Similar in general form to larval *R. blythi.* Head-body width .60–.70 of head-body length, depth .58–.70 of width; eyeball .10 of head-body length (Stages 33–36); width of oral disk .20–.34 of head-body width; snout–spiracle .47–.51 of head-body length; tail length 1.6–2.1 times head-body length, maximum depth .26–.31 of tail length. Lower lip with short, thick marginal papillae in single continuous row, 4–6

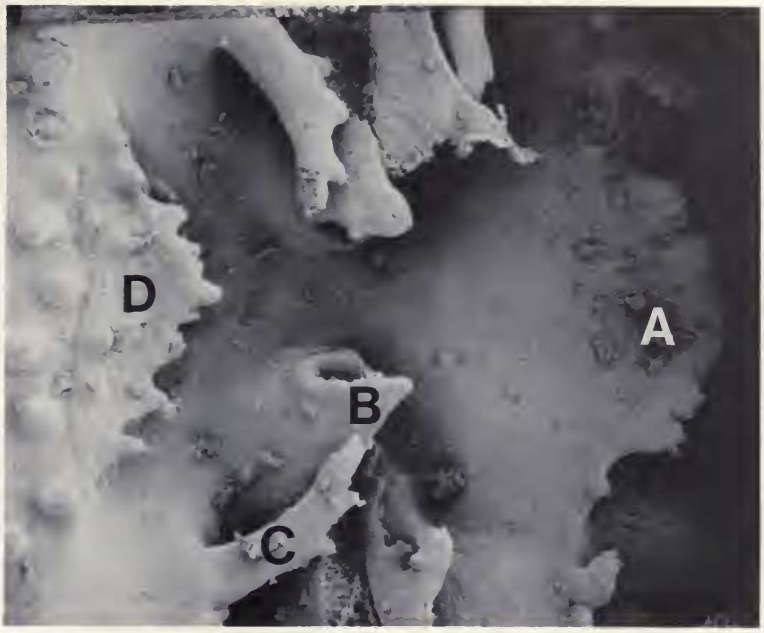

FIG. 25. *Rana ingeri.* Anterior portion of roof of buccal cavity (× 110), anterior to right. **A,** Prenarial ridge; **B,** projection of posterior narial wall; **C,** postnarial papilla; **D,** median ridge.

short inframarginal papillae in lateral third of lower lip; denticles I:1+1/1+1:II, outermost lower row one-third to half length of middle row; beaks black in marginal third, finely serrated (fig. 27), upper without median convexity. Lateral line pores around eye and in double row dorsolaterally on body and caudal muscle.

Head-body dusky with narrow dark band across back behind level of eyes; band sometimes interrupted; a second, wider dorsal band at end of body; underside of head-body with or without dusting of melanophores; caudal muscle speckled, usually with dark spots dorsally, without pigment ventrally; dorsal fin dusted with melanophores entire length; ventral fin lightly speckled in distal half.

Head-body lengths (mm): 6.2 (Stage 26), 8.3 (Stage 33), 7.5–9.3 (Stages 36–38), 8.7–9.3 (Stage 44). Total length to 25.5 mm (Stage 36).

The denticles are more densely crowded within rows and have longer shafts than those of larval *R. blythi.* There are 4 sharp cusps slightly curved orally, 2 at the very apex and 2 shorter, subapical ones (fig. 26).

Internal Buccopharyngeal (based on FMNH 158029, Stage 36, examined by light microscope and SEM)—Prelingual area of floor (fig. 27) with a large, flattened palp in each posterolateral corner, palps oriented transversely, with 4–6 short, thick marginal projections, palps separated by more than width of base; between palps a cluster of 6 unbranched papillae; 5 short, thick papillae and a clump of fused papillae just inside beak on each side, leaving a smooth median strip. Tongue anlage indefinite except for a long, shallow transverse groove at rear; 4 simple, conical lingual papillae. Buccal floor arena (fig. 28) pentagonal, much wider posteriorly; a group of 15–20 conical papillae in each posterolateral corner; a triangular area of about 100 pustules in center of floor arena, apex just behind tongue anlage, area widening to reach clusters of papillae and extending back almost to margin of velum; a few low pustules lateral to apex of triangle. Buccal pockets narrow, oblique; perforation not evident; median corner of pocket adjacent to anteriormost lateral papillae of floor arena; 4–6 pustules anterior to median corner of pocket. Ventral velum with spicules; no median notch; margin with 6–8 short projections; no secretory pits on margin. Glottis well behind velum. Branchial baskets largely exposed behind velum; 3 gill chambers on each side, oblique, length of middle chamber about .6 of buccal floor behind prelingual area; filter ruffles with tertiary folds; filter canals open.

Prenarial area of roof with slightly arched, transverse row of 7 short, thick papillae, middle one

FIG. 26. *Rana kuhli.* Denticles of middle row of lower lip, aboral surface (× 2,010).

largest and pustulose. Nares oval, transverse, gap between them less than width of one; anterior narial wall low, with short papilla rising from its center; posterior wall higher, median corner drawn out into triangular projection curled forward. Postnarial area with depression behind posterior narial wall; an anteromesad curled papilla behind median area of groove; a short papilla just in front

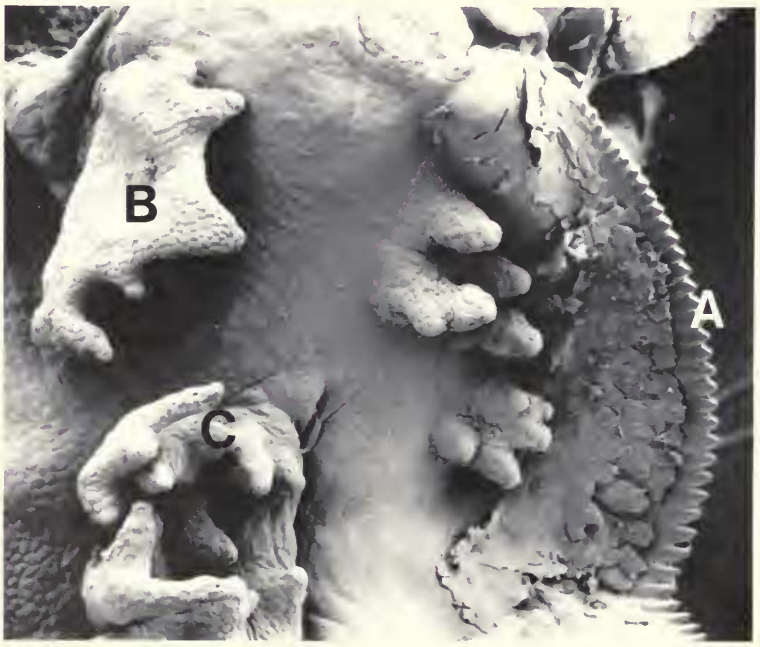

FIG. 27. *Rana kuhli.* Left half of prelingual area of buccal floor (× 130), anterior to right. **A,** Beak; **B,** lateral prelingual palp; **C,** median prelingual palp.

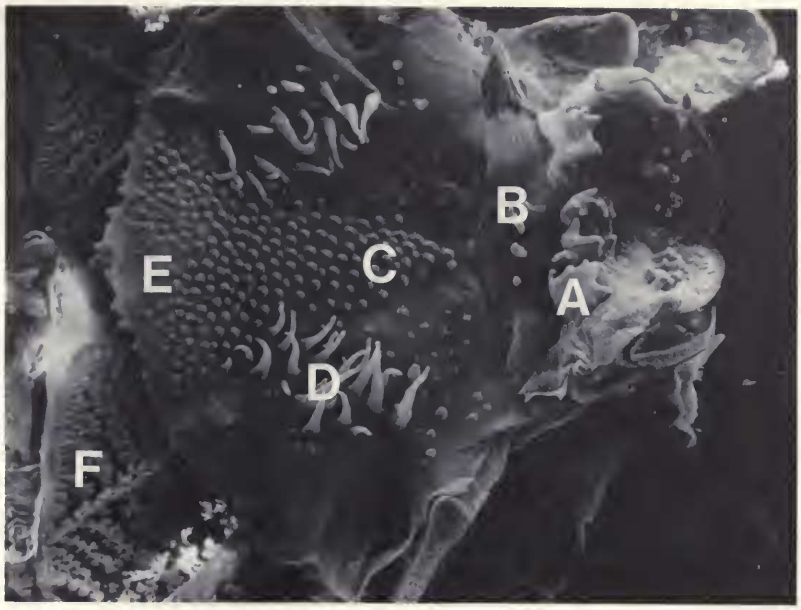

FIG. 28. *Rana kuhli.* Floor of buccopharyngeal cavity (× 39), anterior to right. **A,** Prelingual palp; **B,** lingual papilla; **C,** pustules of buccal floor arena; **D,** lateral papillae of buccal floor arena; **E,** ventral velum; **F,** branchial basket.

of median ridge. Lateral ridge palp flat, oriented anteroposteriorly, 4 long apical projections, height about equal to width of base. Median ridge low, base much greater than height, margin with 4 short projections. Buccal roof arena rectangular; 10 or 11 tall, slender, unbranched papillae in double row on each lateral border; entire interior occupied by more than 100 rounded pustules, slightly denser and smaller posteriorly. Glandular zone visible laterally, central area damaged. Dorsal velum with 10 slender projections medially and about 8 short ones laterally on each side.

ECOLOGICAL DISTRIBUTION—Distribution of larval *R. kuhli* in Borneo is not clear from our few samples, most of which were obtained in slowly flowing or standing water and with other kinds of tadpoles (table 16).

REFERRED MATERIAL—FMNH 77554, Kalabakan, Tawau District, Sabah; FMNH 130829, tributary of Sungei Kepungit (740 m), Mt. Kinabalu, Sabah; FMNH 77565–6, Matang, First Division, Sarawak; FMNH 157994–5, 158025–9, Sungei Pesu, Tubau district, Fourth Division, Sarawak; FMNH 96010, headwaters of Baleh River, Seventh Division, Sarawak; FMNH 213884, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

TABLE 16. Microhabitat distribution of larval *Rana kuhli* in forest streams and their occurrence with tadpoles of other species.

Species	No. of samples		
	Protected side pool	Pothole on bank	Seepage on bank
Leptobrachium nigrops	1	...	...
Megophrys nasuta	1	...	1
Rana blythi	1	...	...
Rana chalconota	1	...	...
Rana ibanorum	...	...	2
Rana ingeri	...	...	1
Polypedates colletti	1	...	...
Without other tadpoles	0	2	0
Total samples	3	2	2

Rana laticeps Boulenger

Association of this tadpole with *R. laticeps* is based on weak evidence. The single larva was caught in a seepage area at the head of a very small stream along with 3 adult *laticeps.* The larva has the denticular array on the lower lip characteristic of larvae of *R. blythi* and related species: a very short outer row, a long continuous middle row, and a narrowly interrupted inner one. It resembles

larval *blythi* in having only a single row of denticles on the upper lip and in having denticles spaced rather than crowded within rows. But it differs from larval *blythi, kuhli, ibanorum,* and *ingeri* in having a very wide lower lip, the portion between the denticles and the margin being almost as wide as the rest. Like larval *kuhli,* it has inframarginal papillae on the lower lip, but whereas in *kuhli* these are restricted to the lateral third of the lip, in this form they extend to the center of the lip. If, as seems likely, this tadpole is not conspecific with any of those forms mentioned above, association with *laticeps* is predicated on two circumstances: *laticeps* is the only Bornean member of this group of species whose larva is unknown, and *laticeps* uses the microhabitat in which this tadpole was found.

DESCRIPTION—**External**—Generally similar to larval *R. blythi.* Head-body width .54 of head-body length; eyeball .10 of head-body length (Stage 39); nostril midway between eye and tip of snout; width of oral disk .31 of head-body width; snout–spiracle .58 of head-body length; tail length 2.0 times head-body length. Lower lip with short, thick papillae in crowded row with narrow gap in center; an inner, irregular row of shorter inframarginal papillae from center of lip to corners; portion of lower lip free of denticles wide; denticles I/1+1: II, outermost lower row about half length of middle row; denticles rather widely spaced within rows (as in larval *blythi*); beaks black along margins, finely serrated, upper without median convexity.

Head-body with many irregular, small, dark spots dorsally and laterally, without pigment ventrally; caudal muscle and dorsal fin with dark speckling throughout; ventral fin with pigment only in distal fourth.

Head-body length 7.4 mm (Stage 39). The tadpole is slightly shriveled in preservative.

REFERRED MATERIAL—FMNH 195867, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Rana malesiana Kiew

Association of Malayan larvae with this species is based on a series reared to metamorphosis (Kiew, 1984). Kiew does not say which diagnostic characters of adult *R. malesiana* were present in his young frogs, but presumably coloration and extent of webbing were involved. Larvae have not been reported from Borneo.

DESCRIPTION—**External** (based on Kiew, 1973)—Head-body oval, slightly flattened above; eyes and nostrils dorsolateral (in Kiew's illustrations); interorbital twice internarial distance. Oral disk ventral, subterminal; single row of papillae on lower lip and at corners of upper; denticles I/I or I/II, lost in most of Kiew's specimens; beaks finely serrated. Spiracle sinistral, opening midway between snout and end of body. Anal opening median. Tail twice head-body length, tapering gradually to narrow tip; maximum depth about one-fifth of tail length; dorsal fin deeper than ventral. In life, head-body golden brown mottled with blackish brown; tail with indistinct vertical dark bars or blotches. Total length to 22.9 mm (Stage 39) in a laboratory-reared tadpole.

The lack of denticles in most of the aquarium-reared tadpoles places some doubt on the denticular formula, which differs from those of other larvae in this group of species. The position of the anal tube given by Kiew is unusual for a ranid tadpole not living in swift water.

ECOLOGICAL DISTRIBUTION—Larval *R. malesiana* appears to be limited to small streams, but Kiew (1973) does not give enough information to determine the range of microhabitats.

REFERRED MATERIAL—None examined.

Rana palavanensis Boulenger

Assignment of these larvae to *R. palavanensis* is based upon a developmental series from Stages 27 to 45 in a single sample. From Stage 41 onward, the webbing and expansion of the digit tips are exactly as those in adult *palavanensis,* and in the last stages, the dorsum has the distinctive coloration of *palavanensis.* These larvae are very similar to those of *R. ingeri* in denticular formula, in having at most a narrow median gap in the marginal papillae, and in lacking inframarginal papillae. The only pronounced difference is in the conspicuously convex dorsal margin of the tail in larval *palavanensis* (illustrated in Inger, 1966, fig. 44).

DESCRIPTION—**External**—Generally similar to larval *R. blythi.* Head-body width .58–.63 of head-body length; eyeball .07–.10 of head-body length (Stages 27–39); width of oral disk .22–.31 of head-body width; snout–spiracle .53–.61 of head-body length; tail length 1.8–1.9 times head-body length, maximum depth .24–.25 of tail length. Lower lip with short marginal papillae in single row, continuous or with very narrow median gap; no inframarginal papillae; beaks black in marginal third, finely serrated, upper without median convexity. Lateral line pores not visible.

FIG. 29. *Rana chalconota.* Denticles of outer row of lower lip, oral surface (× 2,100).

Head-body speckled irregularly dorsally and laterally, an obscure bar across root of tail, ventrally without pigment; caudal muscle speckled throughout, with dark longitudinal bars on dorsal margin; dorsal fin with scattered melanophores, densest near tip; ventral fin without pigment except in distal fourth.

Head-body lengths (mm): 7.1–7.3 (Stage 27), 8.2 (Stage 36), 7.9–8.3 (Stages 39–40). Total lengths to 23.6 mm (Stage 40).

These specimens are slightly shriveled, reducing the value of all measurements.

Internal Buccopharyngeal (based on FMNH 139546, Stage 31, specimen slightly dessicated, rendering some observations uncertain)—Prelingual area of floor bounded posteriorly by a flattened palp in each lateral corner and a pair of median, pustulose papillae; papillae about same height as palps and separated from them by distance equal to their own height; anterior to palp a short, thick, pustulose papilla, much closer to palp than latter is to median papilla. Tongue anlage indistinct; 4 conical lingual papillae. Buccal floor arena squarish; 4–5 tall, slender papillae along posterior part of each lateral border; a group of 12 pustules anterior to lateral papillae; posterior two-thirds of interior with ca. 40 rounded pustules. Buccal pockets transverse, narrow; appear to be perforated; no pre- or postpocket pustules or papillae. Ventral velum supported by spicules; one marginal projection laterally; no median notch, but median part of velum wavy. Glottis behind velum. Three gill chambers on each side; filter rows shriveled.

Prenarial area of roof with forwardly arched transverse, pustulose ridge flanked on each side by a short, thick papilla. Nares transverse, oval, widely separated; anterior narial wall slightly raised, with papilla rising from center; posterior narial wall with median valvular expansion. Postnarial area with papilla behind medial corner of postnarial groove. Lateral ridge palp flattened, height greater than width of base; 2 or 3 short, terminal branches. Median ridge low, width 4 times height; margin pustulose. Buccal roof arena squarish; 5 long, slender lateral papillae in a row; entire interior of arena with ca. 75 rounded pustules. Rest of roof damaged.

ECOLOGICAL DISTRIBUTION—Larval *R. palavanensis* appears to be limited to small pools of standing water. One sample was taken from a pool in headwaters of a very small stream with larval *Polypedates colletti,* 1 in a similar microhabitat but without other tadpoles, and 1 tadpole in a water-filled hole in a fallen tree.

REFERRED MATERIAL—BMNH 1978.216, Mt. Mulu National Park, Fourth Division, Sarawak; FMNH 139546, 213883, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Rana chalconota (Schlegel)

Assignment to species is based upon complete developmental series through Stage 44, at which

time the hands and feet have features typical of adult *R. chalconota*: fingers with supernumerary subarticular tubercles, disk of first finger about half size of those of outer fingers, toes fully webbed to disks, outer metatarsal tubercle distinct. At this metamorphic stage, the oval patches of abdominal glands are still present.

DESCRIPTION—**External**—Head-body oval, rounded at snout, slightly flattened above, maximum width between eyes and end of body, .58–.65 of head-body length, depth .67–.70 of width; eyes dorsolateral, not visible from below, eyeball .09–.11 of head-body length (Stages 34–40); interorbital .30–.32 of head-body width, twice diameter of eye, slightly less than eye–snout distance; nostrils lateral, open, rim not raised; internarial subequal to interorbital; nasolacrimal duct usually distinct. Oral disk ventral, subterminal, width .43–.50 of head-body width; lower lip with 2 or 3 crowded, continuous rows of short papillae, 2–4 much larger papillae in lateral quarters of lower lip; upper lip with papillae only at corners; denticles I:3+3/1+1:II or I:4+4/1+1:II, rows of lower lip subequal in length; beaks finely serrated (fig. 30), black near margin, upper with weak median convexity. Spiracle sinistral, midway up side, tube attached to body wall, opening slightly narrower than rest of tube, snout–spiracle distance .59–.69 of head-body length. Anal tube dextral. Tail with convex margins, tapering gradually to rounded tip; tail length 1.6–1.8 times head-body length, maximum depth .26–.31 of tail length; caudal muscle deeper than either fin to midlength; origins of both fins at end of body; dorsal fin deeper than ventral to near tip.

Large glandular patches (see Inger, 1966, fig. 35), each consisting of more than 25 glandules; 1 patch behind eye, 1 dorsolaterally near end of body, and 1 elongate ventrolaterally; a median circular patch usually evident behind oral disk; single glandules scattered over middorsal surfaces; no glands on tail. Lateral line pores not visible.

Color in preservative pale yellowish brown with regular black markings; a small spot on side of snout, a vertical bar below eye, a curved bar laterally, and a circular spot dorsolaterally behind head; tail without markings.

Head-body lengths (mm): 9.4–11.8 (Stages 26–29), 8.5–14.0 (Stages 30–33), 9.2–16.0 (Stages 34–37), 12.2–18.1 (Stages 38–42). Total lengths to 48.1 mm (Stage 42).

The denticles are closely spaced in rows, with the distal two-thirds of the shaft bordered with 12–15 closely spaced triangular cusps (fig. 29). The margins of the shaft are curved toward the mouth, though the shaft itself has only a weak angle.

Internal Buccopharyngeal (based on FMNH 213827, Stage 35, FMNH 139556, Stage 31, and FMNH 213827, Stage 36; last two examined by means of SEM)—Prelingual area of floor narrow, a large flattened palp in each posterolateral corner; palp with concave face forward, margin pustulose, palps narrowly separated; a small median pustule between palps; a curved row of 4–6 pustules or short papillae running forward from each palp (fig. 30). Tongue anlage wide; 2 long, approximated lingual papillae. Buccal floor arena an elongate oval defined by a curved row of 5–7 papillae in each lateral border; interior of arena smooth anteriorly, with about 25 evenly spaced pustules in posterior half. Buccal pockets transverse, curved, not perforated, level of pockets slightly closer to tongue anlage than to rear of velum. About 6–12 pustules behind buccal floor arena; 20–25 pustules anterior to buccal pocket and lateral to floor arena. Ventral velum supported by spicules; no median notch; margin with 5 short projections on each side, the 6 median ones closer together; margin with secretory pits. Glottis fully exposed behind velum. Branchial baskets widely exposed behind velum, slightly oblique; 3 gill chambers on each side; length of middle chamber about two-thirds length of floor behind prelingual area; filter ruffles with tertiary folds; 9–11 filter rows on median wall of middle chamber; filter canals open (fig. 31).

Prenarial area of roof with short, transverse, pustulose ridge midway between beak and nares; 4 low pustules behind ridge. Nares oval, widely separated; anterior narial wall raised, a wide, short, pustulose papilla rising from its center, wall pustulose medially; posterior narial wall smooth with weak median projection into buccal cavity. Postnarial area with a low ridge paralleling each naris; a wide, medially projecting, pustulose papilla at median end of ridge; 2–8 low pustules between and slightly behind ridges; a short, pustulose, transverse ridge immediately before median ridge. No lateral ridge papilla. Median ridge semilunar; much wider than high; margin pustulose. Buccal roof arena oval; 4–7 papillae in staggered row on each lateral border; interior of arena with about 50 evenly spaced, low pustules. A slightly oblique row of 8–9 pustules in extreme lateral portion of roof, beginning behind level of nares and ending opposite middle of buccal roof arena. Glandular zone 4–8 pits deep. Dorsal velum with scalloped margin.

ECOLOGICAL DISTRIBUTION—Larval *R. chalcon-*

FIG. 30. *Rana chalconota.* Beak and prelingual area of buccal floor (× 66). **A,** Beak; **B,** prelingual palp.

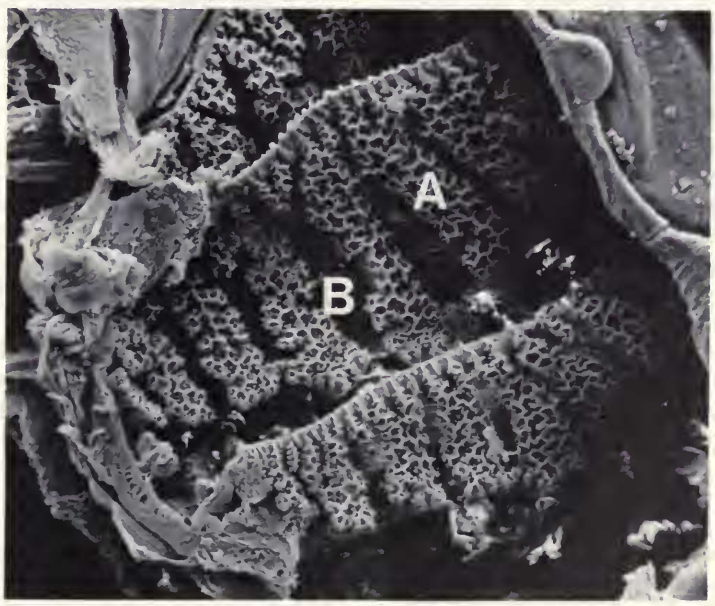

FIG. 31. *Rana chalconota.* Right branchial basket (× 55), anterior to right. **A,** Filter ruffle; **B,** filter canal.

ota is largely restricted to stream microhabitats with weak or no current, and they have been found with a number of other kinds of tadpoles in such situations (table 17).Three small samples were also collected in temporary rain pools in a large clearing at the edge of recently cut forest along the Kalabakan River, Sabah, together with tadpoles of *R. nicobariensis* and *Rhacophorus nigropalmatus.*

REFERRED MATERIAL—FMNH 63519, 63521, Bukit Kretam, Sandakan District, Sabah; FMNH 77529–31, 77543, 77545–47, 77550–1, 77553, Kalabakan, Tawau District, Sabah; FMNH 77567–

TABLE 17. Microhabitat distribution of larval *Rana chalconota* in forest streams and their occurrence with tadpoles of other species.

Species	No. of samples			
	Shingle	Open pool	Protected side pool	Pothole on bank
Leptobrachium montanum	...	1	2	...
Ansonia longidigita	...	...	2	...
Bufo asper	...	...	...	1
Bufo divergens	...	...	4	1
Pedostibes hosei	...	...	2	...
Rana blythi	...	1	11	2
Rana ibanorum	...	...	7	6
Rana kuhli	...	...	1	...
Rana signata	...	...	2	...
Rhacophorus bimaculatus	1	...	1	...
Rhacophorus pardalis	...	...	...	1
Microhyla petrigena	...	...	...	1
Without other tadpoles	0	0	11	1
Total samples	1	2	26	7

70, Matang, First Division, Sarawak; FMNH 121309, Samunsam River, near Sungei Bemban, First Division, Sarawak; BMNH 1978.1672, Mt. Mulu National Park, Fourth Division, Sarawak; FMNH 83025, Long Seniai, Akah River, Fourth Division, Sarawak; FMNH 158008–10, Sungei Pesu, Tubau district, Fourth Division, Sarawak; FMNH 96013–7, 121554, headwaters of Baleh River, Seventh Division, Sarawak; FMNH 139555–61, 139564, 213798–830, 216172, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Rana glandulosa Boulenger

Larvae of this species have not yet been reported from Borneo, despite the large number of adults that have been collected. Assignment of Malayan tadpoles to *glandulosa* was based on similarity of metamorphosing young to adults (Berry, 1972).

DESCRIPTION—**External** (based on Berry, 1972)—Head-body oval, width .50–.58 of head-body length; eyes dorsolateral. Oral disk ventral, subterminal; papillae in uninterrupted double row across lower lip, confined to corners of upper lip; denticles I:2+2/1+1:II; beaks serrated, black at margins. Spiracle sinistral, tube fused to body wall, opening nearer vent than to tip of snout. Anal tube dextral. Tail more than twice head-body length; dorsal margin convex; tip pointed; both fins arising at end of body; dorsal deeper than ventral. Head-body and fins covered with scattered whitish glandules. In life head-body and tail reddish brown, with darker brown patches on body, caudal muscle, and dorsal fin. Head-body length 16 mm, total length 54.8 mm (Stage 34).

Berry states that the external nares are not open until just before metamorphosis, which makes larval *glandulosa* unique among Indo-Malayan ranid larvae.

ECOLOGICAL DISTRIBUTION—The single sample collected by Berry was taken in a small stream at 1,280 m in Pahang, West Malaysia. In Borneo *glandulosa* is known only from the lowlands (Inger, 1966).

REFERRED MATERIAL—None examined.

Rana luctuosa (Peters)

Association with adults was made by Flower (1896) on the basis of a developmental series of Malayan larvae complete through metamorphosis. Bornean tadpoles are essentially identical to the Malayan ones. The larvae named *Rhacophorus* sp. B (Inger, 1966) are included here.

DESCRIPTION—**External**—General form similar to larval *R. chalconota,* but body more robust. Head-body width .59–.73 of head-body length, depth .63–.75 of width; eyeball .07–.08 of head-body length (Stages 26–34); interorbital .42–.51 of head-body width; width of oral disk .29–.42 of head-body width; snout–spiracle .53–.66 of head-body length; tail length 1.2–1.8 times head-body length, maximum depth .30–.46 of tail length. Lower lip with 2–3 continuous, crowded rows of short papillae; external to these an interrupted row of enlarged papillae 2–3 times length of others; denticles I:3+3 to I:5+5 on upper lip, 1+1:III on

lower; rows of lower lip subequal in length. Beaks black in marginal third, finely serrated, upper with weak median convexity. Spiracular tube wide, opening less than half diameter of tube. Both fins proximally with fleshy, thickened areas adjacent to muscle. No glands evident on body or tail. Lateral line pores in 2 longitudinal rows beginning on snout, 1 passing above and 1 below eye; lower row curving dorsad behind eye and both extending onto dorsal portion of caudal muscle.

Color in life purplish black on all surfaces, with yellow-brown spots on sides of body and tail; in preservative brownish or purplish, with indistinct lighter spots.

Head-body lengths (mm): 13.8–19.8 (Stages 26–29), 21.3–24.5 (Stages 34–37), 25.6 (Stage 40). Total length to 47.1 mm (Stage 34).

Internal Buccopharyngeal (based on FMNH 139372, Stage 27)—Prelingual area of floor bounded posterolaterally by a very wide, tall, curved flap with concave face forward, apical margin very irregular; gap between flaps about equal to height of one; on left side flap extended forward laterally; on right side a low, ragged flap narrowly separated from main posterior portion; a narrow, low, curved flap in midline in line with rear of large ones; a median pair of short, conical papillae between anteromedial corners of large flaps; these papillae preceded by low, short, transverse ridge; a transverse row of 4 pustules just inside each half of lower beak; in anterolateral corner of prelingual, a bifurcate, low flap posterior to row of pustules. Tongue anlage indistinct at this stage; 4 tall, slender, juxtaposed lingual papillae across center of area. Buccal floor arena pentagonal, as wide as long; 7–8 short, conical papillae in each posterolateral corner; a single conical papilla anteriorly in lateral border; 40 low pustules rather evenly spaced in rear of interior intermixed with 5 short, conical papillae; a cluster of about 20 low pustules surrounding anterolateral papilla. Buccal pockets transverse, curved, perforated. Ventral velum supported by spicules; no median notch; margin with 5 short, wide projections on each side, lateral ones widely separated and larger; margins and projections with secretory pits. Glottis behind velum. Branchial baskets largely exposed behind velum; 3 gill chambers on each side, oblique; filter ruffles dense, with tertiary folds; 11 filter rows on median wall of middle chamber; filter canals narrow.

Prenarial area of roof with inverted U-shaped row of large pustules in center; a longitudinal row of pustules and short papillae running down middle of U. Nares oval, transverse, separated by about half length of one; anterior narial wall laterally very low with 2–3 pustules; a medially curved, flattened, pustulose papilla rising from center of wall; median third of wall raised; posterior narial wall thin, low laterally, medially with obtusely triangular, valvular projection. Postnarial area with a depression behind each naris; rear margin of depression with 3–5 low pustules laterally and a tall, flattened, curved, pustulose papilla medially; 5 low papillae or pustules in a transverse group before median ridge. No lateral ridge papilla. Median ridge low, rounded, with pustulose margin; height less than one-third width. Buccal roof arena oval, width about two-thirds length; 10 short, conical papillae in staggered, curved row on each lateral border; 50–60 pustules evenly spaced throughout interior. A short, conical papilla in far lateral edge of roof opposite middle of buccal roof arena. Glandular zone deep, continuous across roof. Dorsal velum with weakly pustulose margin.

ECOLOGICAL DISTRIBUTION—Appears to be restricted to pools of standing or slowly flowing water. Three samples were found in pig wallows on forested ridges, 1 with larval *Rhacophorus dulitensis* and *Microhyla borneensis* and a second with those forms plus larval *Microhyla* sp. C. Dring (*in litt.*) collected a small sample from shallow pools of an intermittent stream. In the Malay Peninsula, they have been found in water-filled road ruts (Grandison, 1972). In Borneo larvae have been collected from near sea level to 915 m (Smith, 1931).

REFERRED MATERIAL—FMNH 77562, Kalabakan, Tawau District, Sabah; ZRC 1.710–12, Kiau, Mt. Kinabalu, Sabah; FMNH 137952, 139372, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak; BMNH 1978.1675, Mt. Mulu National Park, Fourth Division, Sarawak.

Rana signata (Günther)

Assignment of these larvae to *R. signata* is based upon developmental series (Stages 25–42) in which the most advanced individuals have partially acquired the distinctive coloration of adult *signata* while still retaining the distribution of dermal glands seen in younger tadpoles.

DESCRIPTION—**External**—More slender and flatter dorsally (see Inger, 1966, fig. 48) than larval *R. chalconota*. Head-body width .59–.70 of head-body length, depth .72–.76 of width; eyeball .08–.11 of head-body length (Stages 31–41); interorbital .30–.40 of head-body width; width of oral disk .33–.41 of head-body width; snout–spiracle

FIG. 32. *Rana signata.* Denticles of inner row of lower lip (× 2,160), oral surface.

.63–.73 of head-body length; tail length 1.9–2.2 times head-body length, maximum depth .20–.24 of tail length. Lower lip with single crowded, continuous row of short papillae; no distinctly enlarged papillae. Denticles I:2+2 or I:3+2 on upper lip, 1+1:II on lower; rows of lower lip subequal. Beaks black at margins, finely serrated, upper with weak median convexity. Spiracular opening constricted to half diameter of tube. Caudal muscle heavy, deeper than either fin until distal fourth.

Glands conspicuous; a wide glandular band around oral disk; a separate, circular patch of glands behind oral disk; a long, narrow ventrolateral band; a small patch anteroventrad from eye; a long dorsolateral band from behind eye to end of body; glandules distributed full length of both fins but absent on caudal muscle. Lateral line pores not visible.

Head-body and tail dark dorsally and laterally; ventral surface of head-body and ventral fin without pigment. Head-body black in life.

Head-body length (mm): 10.2 (Stage 31), 12.9 (Stage 37), 10.6–13.5 (Stages 39–41). Total length to 41.1 (Stage 37).

The denticles (fig. 32) are very similar to those of *R. chalconota.*

Internal Buccopharyngeal (based on FMNH 213788, Stage 37)—Prelingual area of floor with large, curved, flattened palp in each posterolateral corner; palp with concave face forward, 4–6 thick, terminal projections; a pair of thick papillae mesad from palps. Tongue anlage low, wide; 4 conical lingual papillae. Buccal floor arena with 6–8 thick, conical papillae in irregular curved row on each lateral border; anterior lateral papilla surrounded by group of low pustules, extending from near center of floor arena to prepocket area; posterior two-thirds of interior with about 30 low, evenly spaced pustules; posterior boundary of floor arena ill defined, a few short papillae grading into pustules extending onto velum. Buccal pockets strongly curved, transverse. Ventral velum supported by spicules; no median notch; 12 short, thick marginal projections medially; laterally 4 short marginal projections on each side; marginal projections with secretory pits. Glottis under velum. Branchial baskets extending well behind velum; 3 gill chambers on each side, oblique; filter ruffles with tertiary folds; filter canals narrowed but open.

Prenarial area of roof with forwardly arched, pustulose, transverse ridge; 1 short, thick papilla laterally, well separated from transverse ridge. Nares transverse, oval, closely approximated; anterior narial wall slightly raised, a thick pustulose

papilla at its center; posterior narial wall higher, with a large pustulose papilla at its medial corner and 2 low papillae laterally. Postnarial area with 2 or 3 low pustules behind each naris; a pair of pustules in front of medial ridge. Lateral ridge papilla absent. Median ridge a truncate triangle with 4 short projections on apex; basal width greater than height. Buccal roof arena with 4–5 low papillae laterally on each side; interior of roof arena fully occupied with 75–90 evenly spaced, slightly pointed pustules, lateral ones tallest. Glandular zone obscured in dissection, but present. Dorsal velum with weakly scalloped margin laterally; margin with secretory pits.

ECOLOGICAL DISTRIBUTION—Larval *signata* is centered in areas of weak current in small streams where they occur with a variety of other tadpoles, particularly those of *R. blythi* and *Ansonia longidigita* (table 18).

TABLE 18. Microhabitat distribution of larval *Rana signata* in forest streams and their occurrence with tadpoles of other species.

Species	No. of samples		
	Riffle	Leaf drift	Protected side pool
Megophrys nasuta	1	...	...
Leptobrachium gracilis	1	...	...
Leptobrachium montanum	...	...	1
Leptobrachella mjobergi	1	...	...
Ansonia longidigita	...	8	3
Bufo divergens	...	...	1
Pedostibes hosei	...	4	1
Rana blythi	...	8	4
Rana chalconota	...	...	2
Rana ibanorum	...	...	2
Rhacophorus bimaculatus	1	...	1
Rhacophorus gauni	...	1	...
Rhacophorus sp.	...	1	...
Without other tadpoles	0	0	1
Total samples	1	8	6

REFERRED MATERIAL—FMNH 77555, 77560, Kalabakan, Tawau District, Sabah; FMNH 77575, Sungei Entunau, Baleh River, Seventh Division, Sarawak; FMNH 77577, 77585, Nanga Putai, Baleh River, Seventh Division, Sarawak; FMNH 139547, 146730, 213787–97, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Ooeidozyga

Larvae of this genus are distinguished from those of other Asian ranids by their peculiar oral disk, which is terminal and has a very narrow upper lip, a protruding, horseshoe-shaped lower lip lacking papillae, and heavy beaks, but no denticles (Smith, 1930). Two species of this genus are known from Borneo, although larvae of one (*laevis*) have not yet been discovered there. The description of larval *laevis* given below is based on tadpoles from Thailand. Larval *baluensis* differ externally from tadpoles of *laevis* mainly in lacking spots on the ventral fin and lower fins. Internally, larval *baluensis* have smaller, more widely separated narial openings and a rounded rather than a triangular prenarial pad.

Ooeidozyga baluensis (Boulenger)

Association of these 4 larvae with *O. baluensis* is based on three considerations. First, they have an oral disk typical of the genus. Secondly, all were collected in forest floor seepages, the microhabitat in which many adult *baluensis* were caught. Finally, these premetamorphic tadpoles (Stages 40–43) have emarginate webbing, which distinguishes *baluensis* from Bornean *laevis*.

DESCRIPTION—**External**—Head-body oval, flat above, maximum width .62–.65 of head-body length, depth .64–.71 of width; eyes dorsolateral, not visible from below, eyeball .15 of head-body length; interorbital slightly greater than length of eye; nostrils open, small, anteromesad from eyes, internarial narrower than interorbital. Oral disk terminal, narrow, .26–.29 of head-body width; no papillae or denticles; upper border of disk a knob-like structure, superficially not differentiated from rest of snout; lower lip horseshoe-shaped, oriented vertically, protruding, surface weakly wrinkled, separated from snout by deep groove. Beaks set back deeply in oral disk, black, heavy, finely serrated, upper with weak median convexity. Spiracle sinistral, midway up side; tube free of body wall; snout–spiracle distance about two-thirds of head-body length. No anal tube in these advanced tadpoles. Lateral line system visible (at 50×) only in supraocular area. Tail long, slender, 2.7 times head-body length; maximum depth .12 of tail length; fins reduced, both much less than depth of caudal muscle except near tip, both originating well behind end of body; dorsal fin with visible capillary network.

Color in preservative pale tan; a faint dark streak

along anteroventral corner of eye, extending forward on snout; a dark vertical bar below eye; parietal area dark; caudal muscle and dorsal fin with small dark spots; ventral fin immaculate.

Head-body lengths (Stages 40–42) 7.1–7.5 mm, total length 26.3 mm.

Internal Buccopharyngeal (based on dissection of FMNH 203447, Stage 40)—Prelingual area of floor as long as wide, slightly narrowed posteriorly, no pustules or papillae, area closed off by deep transverse flap continuous with lateral walls of floor. Tongue anlage long, pointed in rear; no lingual papillae. Buccal floor arena ill defined, surface smooth except for shallow median groove continuous anteriorly with grooves flanking tongue anlage. No projections from floor behind prelingual. Rear of floor damaged.

Prenarial area of roof largely occupied by a wide U-shaped, raised pad, rounded and with free margin anteriorly; rear of pad merging into narial area. Nares small, round, situated far laterally, openings separated by more than width of one; anterior narial wall drawn out into anteriorly directed, triangular flap, the median corner of which reaches much farther toward midline than narial opening; posterior narial wall low. No median ridge, lateral ridge papilla, or other projections from roof.

The absence of buccal papillae, median ridge, and lingual papillae is a striking feature of the oral cavity. Although the small sample size prevents dissection of the gut, the form of the oral disk suggests that larval *O. baluensis* are macrophagous carnivores, as are tadpoles of *O. laevis* and *O. lima* (Smith, 1916). This being the case, reduction of the usual particle sorting apparatus is not surprising, as the same phenomenon occurs in macrophagous tadpoles of other families (Wassersug, 1980). An alternative possibility is that the reduction is an ontogenetic result of the late stage (40) of the dissected tadpole. Probably this alternative can be rejected, as Wassersug (1976) observed that in larval *Hyla regilla* most oral papillae do not begin to degenerate until Stage 42 or 43.

Ecological Distribution—Apparently restricted to forest floor seepages. Although our notes do not record depth of water, in most such places, water is rarely 1 cm deep. Consequently, these tadpoles probably live much of the time partly out of water. No other kinds of larvae were found with them.

Referred Material—FMNH 203447, 203455, 203481–2, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Ooeidozyga laevis (Günther)

Association of these Thai tadpoles with adults of *O. laevis* is based on complete developmental series in which terminal stages have the characteristics of adult *laevis*. They agree with larvae assigned to this species by Smith (1916). I assume Bornean larvae will prove to be identical to these.

Description—**External**—Similar to larval *O. baluensis*. Head-body width .58–.67 of head-body length, depth .61–.70 of head-body width; eyeball .13–.15 of head-body length (Stages 38–42); interorbital .25–.29 of head-body width; width of oral disk .15–.16 of head-body width; snout–spiracle .74–.77 of head-body length; tail length 1.9–2.7 times head-body length, maximum depth .14–.15 of tail length. Oral disk as in larval *baluensis*. Head-body with obscure dark spots; both fins with strong dark spots along margins.

Head-body length 8.5 mm, total length 23 mm (Smith, 1916).

Internal Buccopharyngeal (based on FMNH 187800, Stage 41)—Prelingual area of floor bordered at rear by continuous, transverse flap, margin of flap with weak irregularities; remainder of prelingual smooth.Tongue anlage distinct, much longer than wide, pointed at rear; no lingual papillae. A series of low, transverse ridges between tongue anlage and prelingual flap, ridges longer than width of tongue anlage. Buccal floor arena poorly defined; 4 low, widely spaced papillae on left border, none on right; 3 pustules in a curved row from right rear corner forward into interior, none on right side. Buccal pockets transverse, wide, not perforated. Ventral velum without spicules; margin straight, angling sharply forward at lateral corners; a few weak marginal pustules laterally, otherwise smooth; no secretory pits evident (50×). Glottal area damaged. Branchial baskets small, restricted to lateral thirds of pharyngeal area; 3 gill chambers on each side, medial one very small; filter surfaces reduced to a few knobs.

Prenarial with a wide, triangular, horizontal flap projecting forward from just before level of nares, apex of flap midway between beak and level of nares. Nares transverse, wide, gap between them about half length of one; anterior narial wall thin, tall, middle expanded into forwardly projecting triangular flap; flap with several small pustules on medial side; lateral portion of anterior wall with 3 or 4 rounded pustules; posterior narial wall low, smooth except for small, rounded expansion in center. A weak depression behind each naris. No lateral ridge papilla, median ridge or other pro-

jections from roof behind nares. Glandular zone not evident. Dorsal velum low, smooth.

Amolops

There are now eight distinct forms of *Amolops* larvae known from Borneo, all immediately recognizable by their abdominal sucker. The sucker, which occupies essentially the entire ventral surface of the body behind the oral disk, has raised lateral and posterior borders. These raised margins begin immediately behind the lateral corners of the oral disk. In almost all forms, there is a band of keratinized tissue just inside the lateral and posterior margins of the sucker and usually an oval or round patch of similar material on each side just medial to the inframarginal band in the front half of the sucker.

Only four of these larval forms can be assigned to adults: those of *cavitympanum* (Boulenger, 1893), *phaeomerus, poecilus,* and *kinabaluensis.* Three of the unassigned forms have an outer metatarsal tubercle in premetamorphic stages and, therefore, cannot be larvae of *A. kinabaluensis* (Inger & Gritis, 1983). Certain identification of larval *A. jerboa, sensu stricto,* is not possible now because all tadpoles collected at the type locality are in early stages of development (Stages 25–26), preventing decisive comparison with the other forms.

Larval *A. cavitympanum* differ externally from the other Bornean tadpoles in the form of its beaks. Unlike the others, its beaks are undivided (see fig. 51, Inger, 1966), smooth externally, and finely serrated (more than 80 serrae on upper beak). In these respects it resembles the tadpole of *A. larutensis* from Malaya. The buccal cavity of larval *cavitympanum* also differs in several ways from those of the others: larval *cavitympanum* has lingual papillae, the others do not; larval *cavitympanum* lacks the prenarial oval pads present in the others; larval *cavitympanum* has short papillae and pustules in the buccal roof arena, the others do not. In each of these distinguishing features, larval *cavitympanum* has character states more closely resembling generalized ranid larvae. But *cavitympanum* has one character state that represents a more derived condition than that in the other Bornean forms: its abdominal sucker has a transverse band of keratinized tissue just behind the oral disk, suggesting a slightly different mode of gripping the substrate.

As Bornean larval *Amolops* share many characters, complete descriptions will be given for only two forms, *cavitympanum* and *phaeomerus.* For the others, I will cite only meristic and mensural features and those characters in which they differ from *phaeomerus.* The description of the abdominal sucker at the beginning of this section applies to all forms with only trivial exceptions, which are cited where needed.

Amolops cavitympanum (Boulenger)

Association of these tadpoles with adults is based on a complete developmental series. Transforming young with the oral disk and abdominal sucker typical of this form have legs with the coloration characteristic of adults (Boulenger, 1893; Inger, 1966; fig. 51 of latter reference has illustrations of entire tadpole).

DESCRIPTION—**External**—Head-body oval, broadly rounded at snout, flat below, maximum width just behind eyes .62–.68 of head-body length; depth .49–.52 of width; eyes dorsolateral, not visible from below, pointing outward, eyeball .09–.10 of head-body length (Stages 36–41); interorbital 2–2.6 times eye diameter; eye–snout distance .38–.39 of head-body length; nostrils open, rim not raised, much closer to eye than to tip of snout; internarial about .8 of interorbital.

Oral disk ventral, width .84–.89 of head-body width; upper lip separated from snout by a groove; upper lip crenulate rather than papillate in lateral fourth or fifth; lower lip with an irregular margin. Denticles III:8+8 or III:9+9 on upper lip, 1+1:IV or 1+1:V on lower. Beaks heavy; upper two-thirds, lower completely black; outer surface smooth; margin very finely serrate, more than 100 serrae on upper beak; upper beak M-shaped, lower V-shaped; neither beak divided. Abdominal sucker as described above; an interrupted transverse band of keratinized tissue just behind oral disk. Spiracle sinistral; tube long, length subequal to depth of body, pointing upward and backward, free of body wall for half its length. Anal tube median, free of tail. Tail heavily muscled, dorsal margin strongly convex, deepest just before middle, tapering to pointed tip; tail length 1.6–1.9 of head-body length, maximum depth .27–.29 of length; caudal muscle deeper than fins in basal half; dorsal fin origin just behind body, fin deeper than ventral fin except in final third; ventral fin origin at end of proximal third of tail.

Head-body with 2 or 3 pairs of glandular clusters; a postocular cluster about an eye length behind eye with 2 or 3 glands; an oblique row of 6–9 glands beginning just below origin of spiracular tube and running upward and backward; a pre-

TABLE 19. Head-body lengths (mm) of larval *Amolops* from Nanga Tekalit, Sarawak. Sample sizes in parentheses.

Stages	Head-body lengths		
	Amolops cavitympanum	*Amolops phaeomerus*	*Amolops poecilus*
26–29	14.0–18.9 (2)	8.2 (1)	6.6–9.5 (8)
30–33	...	9.5–11.5 (12)	7.7–9.3 (2)
34–37	20.0–22.2 (3)	10.4–14.7 (32)	10.3–11.9 (6)
38–40	22.6–24.5 (6)	12.3–15.3 (14)	11.2–12.3 (5)

spiracular group of 2 glands present in some individuals. No glands in fins.

Head-body without spinules or other protuberances. Lateral line pores visible; 2 longitudinal rows beginning on snout; 1 running below nostril and eye; second running above nostril and eye and continuing onto dorsal margin of caudal muscle; a short branch from second curving down behind eye.

Head-body dark gray dorsally and laterally, with small light spots; caudal muscle dark with light spots; fins dark, with light band along base and light spots on margins.

The denticles have the same shape as those of *A. phaeomerus* (see below), but have more serrations (24–28).

Head-body lengths in Table 19. Total lengths to 68.5 mm (Stage 39).

Internal Buccopharyngeal (based on FMNH 213748, Stage 37)—Prelingual area of floor with a small papilla in posterolateral corner. Tongue anlage conspicuous, longer than wide, pointed at rear; 2 slender lingual papillae in its center. Buccal floor arena smooth except for 2 or 3 forked papillae in posterolateral corner near buccal pocket and a row of short papillae or pustules across rear border. Buccal pocket transverse, narrow, long, not perforated; level of pockets closer to rear of velum than to level of tongue anlage. Ventral velum supported by spicules; margin smooth except for 2 short projections on each side; no secretory pits on dorsal surface. Glottis completely exposed behind velum. Branchial baskets moderate; length of middle chamber about two-thirds of distance between tongue anlage and rear of velum; 11 filter rows on medial wall of middle chamber; filter rows with tertiary folds; filter canals overarched.

Prenarial area of roof with 6–10 pustules clustered about a short median ridge near center; rest of area smooth. Nares transverse, narrow, separated by about two-thirds length of one; anterior wall thick, low, with a pustulose, medially curved, short papilla arising from its center; posterior narial wall taller, thin. Postnarial area with 1 tall, thick, pustulose papilla behind median corner of each naris; papillae projecting forward. No lateral

TABLE 20. Microhabitat distribution of larval *Amolops* in forest streams at Nanga Tekalit, Sarawak, and their occurrence with tadpoles of other species.

Species	No. of samples					
	Amolops cavitympanum	*Amolops phaeomerus*		*Amolops poecilus*		
	Torrent	Torrent	Riffle	Torrent	Riffle	Shingle
Leptobrachium gracilis	...	...	1	...	...	...
Leptobrachium montanum	1	1	1	1	...	...
Megophrys nasuta	...	1	1	1	1	1
Ansonia albomaculata	1	1	...	1	...	...
Bufo asper	1	...	...	...	...	...
Amolops cavitympanum	...	2	...	1	...	...
Amolops phaeomerus	2	...	...	4	1	...
Amolops poecilus	1	4	1	...	...	...
Rana blythi	...	...	...	1	1	...
Rhacophorus bimaculatus	...	1	1	1	1	2
Without other tadpoles	1	5	1	2	0	0
Total samples	4	10	3	7	4	2

FIG. 33. *Amolops phaeomerus.* Denticles of outermost row of lower lip, aboral surface (× 2,640).

ridge papilla. Median ridge narrow, about half height of postnarial papilla; tip with pustules. Buccal roof arena full width of mouth, with 5 short papilla in each lateral border; a transverse row of pustules forming posterior border of arena. Glandular zone very narrow. Dorsal velum with smooth margin; posterior face densely set with low, rounded projections.

ECOLOGICAL DISTRIBUTION—Distribution and association with other types of tadpoles are given in Table 20. The highest known elevation for larval *cavitympanum* is 300 m.

REFERRED MATERIAL—BMNH 93.5.30.27, Bongon, Kudat District, Sabah; FMNH 83021 and Sarawak Museum unnumbered, Long Seniai, Akah River, Sarawak; FMNH 83022, Meligong, Akah River; FMNH 136335, 213746–48, Nanga Tekalit, Seventh Division, Sarawak.

Amolops phaeomerus Inger and Gritis

Association of this larval form with adults of *Amolops phaeomerus* is based on a complete developmental series from young tadpoles (Stage 26) to transforming young. Two transforming juveniles (snout–vent 14.0–15.8 mm) still retain the distinctive color pattern and body glands of this kind of tadpole while having the fully webbed toes, expanded tips of digits, and coloration of the thigh characteristic of adult *A. phaeomerus* (Inger & Gritis, 1983). See illustrations in Inger (1966, fig. 52).

DESCRIPTION—**External**—Head-body oval, broadly rounded at snout, flat below, maximum width between eyes and end of body; width .66–.74 of head-body length; depth .50–.58 of width; eyes dorsolateral, not visible from below, pointing outward; eyeball .11–.12 of head-body length (Stages 36–38); interorbital twice eye diameter; eye–snout distance .32–.38 of head-body length; nostrils open, rim not raised, dorsal margin with a weak median convexity, slightly closer to eye than to tip of snout; internarial about .7 of interorbital.

Oral disk ventral, width .58–.64 of head-body width; upper lip separated from snout by a groove; upper lip with short marginal papillae in lateral third, inframarginal papillae near corner; lower lip with uninterrupted row of short marginal papillae. Denticles III:3+3/1+1:V, decreasing in size from inner rows outward. Beaks extremely heavy, completely black, outer surfaces ribbed; upper beak M-shaped, lower V-shaped; keratinized portions of both beaks divided; each half of upper with 5–8 very coarse serrae, each half of lower with 5–8. Abdominal sucker as described above (p. 61); no transverse band of horny tissue behind oral disk. Spiracle sinistral, low on side; snout–spiracle distance .69–.74 of head-body length; tube long, pointed slightly upward, free of body wall for about half its length. Anal tube median, free of tail.

Tail heavily muscled, dorsal margin convex, deepest near midlength, tapering in final third to pointed tip; tail length 1.39–1.46 of head-body

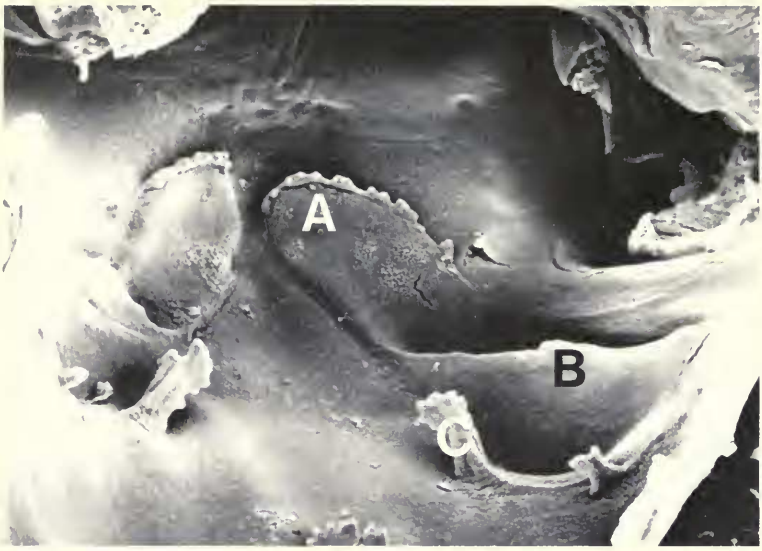

FIG. 34. *Amolops phaeomerus*. Narial region of buccal roof (× 50), anterior at top. **A,** Prenarial pad; **B,** posterior narial wall; **C,** postnarial papilla.

length, maximum depth .25–.28 of tail length; caudal muscle deeper than fins in proximal three-fifths; dorsal fin origin just behind end of body, deeper than ventral fin except at tip; origin of ventral fin at end of proximal third of tail.

Head-body with 4 pairs of glandular clusters; juxtoral cluster with 4–7 glands, prespiracular with 7–10 glands, postocular with 2–4, cluster at end of body midlaterally with 21–27. No glands in fins.

Head-body without spinules or other protuberances. Lateral line pores visible around dorsal and posterior borders of orbit and on dorsal portion of root of caudal muscle.

Yellowish green in life, with large, well-defined black spots on head-body and caudal muscle; fins dusky. In preservative light areas turn straw-color.

The denticles are strongly curved or bent toward the mouth and are completely margined with 13–17 short, wide cusps. These projections are sharp when a denticle first comes into position, but are blunted by wear before the denticle is shed (fig. 33).

Head-body lengths in Table 19. Total length to 34.3 mm (Stage 37).

Internal Buccopharyngeal (based on FMNH 136333, Stages 36–37, and FMNH 136325, Stage 37, the last examined by means of SEM)—Prelingual area of floor with 1 low flattened palp on each side in posterior lateral corner; no other projections. Tongue anlage conspicuous, longer than wide, pointed at rear; no lingual papillae. Buccal floor arena with 3–5 short, stubby papillae in rear half of each lateral border, papillae surrounded by 6–8 pustules; 12–15 low papillae and pustules in a transversely oval group extending laterad from posterolateral corner of arena; interior of arena smooth. No other projections from floor of mouth. Buccal pockets transverse, narrow, strongly curved; level of pockets midway between level of tongue anlage and rear of velum. Ventral velum supported by spicules; margin with 3 short projections on each side; a feeble median indentation; no secretory pits on dorsal surface or margin. Glottis just beyond edge of velum. Branchial baskets rather small, mostly exposed behind velum; length of middle chamber about two-thirds of distance between tongue anlage and median margin of velum; 9–11 filter rows on median wall of middle chamber; filter ruffles with tertiary folds; filter canals open.

Prenarial area of roof with a pair of oval, flat pads angling anteromedially from nares (fig. 34), pads with pustulose margins anterolaterally. Nares transverse, widely separated; anterior narial wall not raised; posterior wall tall, thin, valvular. Postnarial area with 1 tall, pustulose papilla behind median corner of each naris; 2 pustules or a short, pustulose papilla laterally. No lateral ridge papilla. Median ridge narrow, height equals width, margin with pustules. Buccal roof arena smooth. Glandular zone wide. Dorsal velum with smooth margin.

ECOLOGICAL DISTRIBUTION—Distribution and association with other types of larvae are given in Table 20.

REFERRED MATERIAL—BMNH 92.9.2.6, Baram River, Fourth Division, Sarawak; BMNH 1933.6.20.1–3, Sungei Leju, Fourth Division, Sarawak; FMNH 96012, Sungei Sedempah, upper Baleh River, Seventh Division, Sarawak; FMNH 136330, 136333, Sungei Laie, upper Baleh River, Seventh Division, Sarawak; FMNH 136324–9, 136331, 213637–45, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Amolops poecilus Inger and Gritis

Assignment of these tadpoles to this species is based on a developmental series, including transforming young that have aspects of the coloration of adult *poecilus* while retaining larval characteristics (Inger & Gritis, 1983).

DESCRIPTION—**External**—Generally similar to larval *A. phaeomerus*. Head-body width .81–.89 of head-body length; depth .56–.62 of width; eyeball .13–.15 of head-body length (Stages 35–39). Oral disk width .52–.59 of head-body width; denticles III:3+3/1+1:IV, lower lip 1+1:V in a few individuals; beaks as in *A. phaeomerus*, each half of upper beak with 5–8 coarse serrae, each half of lower with 4–7. Tail length 1.69–1.90 times head-body length, maximum depth .29–.35 of tail length.

Head-body with 4 pairs of glandular clusters; juxtoral one with 1–3 glands, prespiracular with 1–2, postocular with 2, and posterior midlateral cluster with 2–4. Ventral fin with 2–6 glands in stages beyond 27. Anterior part of head-body with whitish spinules laterally in stages beyond 37.

Head-body brownish in preservative, with obscure dark spots; caudal muscle dark with narrow vertical light bars or with light and dark areas subequal; no pigment ventrally on caudal muscle.

The denticles have the same shape as those of *A. phaeomerus*.

Head-body lengths in Table 19. Total length to 35 mm (Stage 38).

Internal Buccopharyngeal (based on FMNH 136323, Stage 36)—Similar to *A. phaeomerus* except in following details. Prelingual area without projections. Tongue anlage rounded in rear. Buccal floor arena with 3–4 short papillae in curved row in posterior half of each lateral border; papillae set in a longitudinal band of 20–25 very small pustules; interior of arena smooth. Ventral velum with 2 weak marginal projections on each side. Ten filter rows on medial wall of middle gill chamber.

Prenarial area of roof with a low, angular, pustulose ridge; prenarial oval pads as in *A. phaeomerus*. Postnarial area with 1 short, pustulose papilla medially behind naris and a group of 5–6 pustules and 1 very short papilla laterally. Glandular zone narrow.

ECOLOGICAL DISTRIBUTION—Distribution and co-occurrence with other larval forms are given in Table 20.

REFERRED MATERIAL—BMNH 92.9.2.4–5, Baram River, Fourth Division, Sarawak; FMNH 158004, Sungei Pesu, Tubau district, Fourth Division, Sarawak; FMNH 136322–3, 136332, 146195, 213646–53, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Amolops kinabaluensis Inger

Association of these tadpoles with *A. kinabaluensis* is based on a developmental series ending in a Stage 41 larva. This individual, which has fully developed hind limbs, lacks an outer metatarsal tubercle, a diagnostic characteristic of *kinabaluensis*. All of the tadpoles grouped here have an undivided, ribbed lower beak having more than 16 coarse serrae, except for 1 Stage 28 larva that has only 12. I am not certain that all are in fact conspecific because of their complex variation. Those from near Tambunam, Sabah, in Stages 31, 32, 35, and 41 have the head-body densely covered with spinules dorsally and laterally; 1 in Stage 28 has them only laterally on the snout. Three in Stages 27, 30, and 31 from 50 km to the north on Mt. Kinabalu, the type locality of *A. kinabaluensis*, lack spinules. All 5 from Tambunam have a cluster of large glands, numbering 2–5, at the end of the body midlaterally; only 1 (in Stage 30) of the 3 from Kinabalu has a cluster of glands (5) in that position. The same Kinabalu larva is the only 1 of these 8 tadpoles from Sabah that has glands (8) in the ventral fin. A tadpole in Stage 39 from the Akah River, Sarawak, has well-developed spinules on the head-body, 8 glands in a cluster at the end of the body, and 7 in the ventral fin.

Two tadpoles from Mt. Mulu, Sarawak (BMNH 1978.1626–27, Stages 34 and 41), probably are not conspecific with the rest, though agreeing with them in the condition of the lower beak. The older of these 2 has an outer metatarsal tubercle, which seems to eliminate treating them as larval *A. kinabaluensis*. Both of them have a glandular cluster at the end of the body, glands in the ventral fin,

spinules on the head-body, and an undivided lower beak with 23–24 coarse serrae. They are not included in the descriptive notes that follow.

DESCRIPTION—**External**—Similar in general form and most details to larval *A. phaeomerus*. Head-body width .57–.70 of head-body length, depth .54–.60 of width, eyeball .10–.11 of head-body length (Stages 30–35). Oral disk width .54–.76 of head-body width. Denticles III:3+3 or III:4+4 on upper lip, 1+1:V or 1+1:VI on lower. Each half of divided upper beak with 11–19 serrae; lower beak not divided, 18–26 coarse serrae (Stages 27–41), 12 in 1 Stage 28 larva. Tail 1.56–1.94 times head-body length, maximum depth .24–.27 of tail length.

Head-body with 3 or 4 glandular clusters; juxtoral cluster with 3–5 glands, prespiracular with 1–5, postocular with 2–6, and posterior midlateral with 0–5. Ventral fins with glands (7) in only 1 larva. Head-body densely covered with spinules dorsally and laterally, except in larvae from Kinabalu sample. Lateral line pores not evident. Head-body brownish with obscure darker markings, caudal muscle and fins dusky or blotched.

Head-body lengths (mm): 12.6–13.6 (Stages 27–28), 13.6–21.0 (Stages 30–33), 21.0 (Stage 35), 19.7–25.0 (Stages 39–41). Maximum total length 66.7 mm (Stage 41).

Internal Buccopharyngeal (based on FMNH 109492, Stage 35)—Similar to *A. phaeomerus* except in following characters. Prelingual area of floor without any projections. Buccal floor arena with a group of pustules at rear. No other projections from floor. Ventral velum with a pair of short projections medially; 2 short projections laterally. Filter rows on median wall of middle gill chamber 11; filter canals overarched by ruffles. Prenarial area of roof as in *phaeomerus*. Postnarial area with a single, pustulose papilla behind medial third of naris.

ECOLOGICAL DISTRIBUTION—Restricted to clear, rocky streams. The known altitudinal range is 185–915 m.

REFERRED MATERIAL—FMNH 83023, Long Seniai, Akah River, Fourth Division, Sarawak; FMNH 109492, Kaingeran River, near Tambunam, Sabah; FMNH 130892–93, Sungei Kepungit, Mt. Kinabalu, Sabah.

Amolops sp. E

Association of these larvae from Mt. Kinabalu is not yet possible. A premetamorphic larva (Stage 41) has an outer metatarsal tubercle, indicating that these are probably tadpoles of a member of the *A. jerboa* species group (Inger & Gritis, 1983). They agree with larval *A. kinabaluensis* in having an undivided lower beak, but differ from that form in having fewer serrae in both beaks, flattened instead of pointed protuberances on the head-body, and glands in the ventral fin of all individuals Stage 28 or older.

DESCRIPTION—**External**—Generally similar to larval *A. phaeomerus*. Head-body width .71–.80 of head-body length, depth .48–.63 of width, eyeball .12–.13 of head-body length (Stages 36–40). Oral disk width .56–.59 of head-body width. Denticles III:4+4/1+1:V in stages beyond 27. Each half of upper beak with 5–9 coarse serrae; lower beak not divided, with 11–16 coarse serrae. Tail 1.54–1.72 times head-body length; maximum depth .26–.30 of tail length.

Head-body with 4 pairs of glandular clusters; juxtoral cluster with 3–6 glands, prespiracular with 3–6, postocular with 3–4, posterior midlateral with 5–8. Ventral fin with 3–7 glands (Stage 27 and older). Lateral and dorsal surfaces of head-body covered with flattened, evenly distributed protuberances, each half size of narial opening; at least those on the snout and below eye brownish. Lateral line pores not evident. Head-body dark brown dorsally and laterally; caudal muscle dark with several irregular, large, light spots or light vertical bars; muscle without pigment ventrally; dorsal fin dusky along margin, ventral fin without pigment.

Head-body lengths (mm): 10.3–10.8 (Stages 27–29), 11.6 (Stage 32), 13.3–14.4 (Stages 35–37), 14.2 (Stage 41). Maximum total length 39.0 mm (Stage 41).

Internal Buccopharyngeal (based on FMNH 130897, Stage 37)—Similar to *A. phaeomerus*, but differing in following features. Prelingual area of floor with a thin, longitudinal ridge laterally just anterior to level of tongue anlage, ridge with 2 short, weakly bifurcate projections. Buccal floor arena with 4–5 very short, stubby papillae in an irregular double row on each side just medial to buccal pockets; 5–6 pustules in a cluster behind papillae. No other projections from floor. Buccal pockets wide; anterior margins closer to level of tongue anlage than to margin of velum. Ventral velum with 2 short projections on each side; no median indentation. Middle gill chamber with 9 filter rows on median wall.

Prenarial area of roof anteriorly with a pair of short, oblique, low ridges, each with 3 short, simple peaks; ridges medial to prelingual ridges of floor. Prenarial oval pads as in *phaeomerus*. Post-

narial area with 1 short, pustulose papilla behind median third of naris; no other projections in this area. Glandular zone narrow.

ECOLOGICAL DISTRIBUTION—Restricted to montane streams from 426–853 m. Field notes refer to rocky pools and riffles.

REFERRED MATERIAL—FMNH 130889, 130894–99. All are from Sungei Mamut, Mt. Kinabalu, Sabah.

Amolops sp. F

Association of these larvae with adults is uncertain, except that they belong to a member of the *A. jerboa* species group (Inger & Gritis, 1983). Three tadpoles in Stage 41 have outer metatarsal tubercles, eliminating *A. kinabaluensis* as the parental form.

DESCRIPTION—**External**—Similar in general form to *A. phaeomerus*. Head-body width .63–.78 of head-body length, depth .48–.59 of width, eyeball .12–.13 of head-body length (Stages 35–38). Oral disk width .57–.65 of head-body width. Denticles III:3+3 on upper lip, 1+1:V or 1+1:VI on lower. Beaks ribbed, both divided, 4–9 coarse serrae on each half of upper, 4–8 on lower. Tail length 1.70–1.88 times head-body length, maximum depth .21–.24 of tail length.

Head-body with 4 pairs of glandular clusters; juxtoral one with 2–4, prespiracular with 1–3, postocular with 1–2, posterior midlateral cluster with 5–11. Ventral fin with a row of 4–8 glands. Head-body covered dorsally and laterally with conical protuberances; area occupied and density of spinules increasing with stage of development; usually not on dorsal surfaces at stages younger than 36; some of spinules tipped with melanin in Stage 40. Lateral line pores visible around dorsal border of eye in some individuals. Head-body dark dorsally and laterally, with faint light blotches in some individuals; caudal muscle dusky, uniform or with light blotches; dorsal fin dusky near margin.

Head-body length (mm): 7.5–10.8 (Stages 26–29), 10.5–12.9 (Stages 30–33), 11.0–13.3 (Stages 34–37), 12.1–15.1 (Stages 38–41). Maximum total length 43.7 mm (Stage 41).

Internal Buccopharyngeal (based on FMNH 130334, Stage 35)—Similar to *A. phaeomerus* except in the following characters. Prelingual area of floor smooth except for a low, fringed, longitudinal ridge on each side just before level of tongue anlage. Buccal floor arena with 7 very short papillae in oblique row on each side. No other projections from floor of mouth. Ventral velum with 2 short, well-separated marginal projections on each side. Median wall of middle gill chamber with 9 filter rows.

Prenarial and narial areas as in *phaeomerus*. Postnarial area with 1 flat, pustulose papilla behind median corner of each naris. Median ridge narrow, taller than wide, margin pustulose.

ECOLOGICAL DISTRIBUTION—Limited to small montane streams, 450–915 m above sea level.

REFERRED MATERIAL—FMNH 130883–86, Sungei Kepungit; FMNH 130888, Sungei Mamut; FMNH 130890, Sungei Balungtungan; FMNH 130891, Sungei Matukungan; FMNH 131242–43, Sungei Liwagu. All localities are small streams on Mt. Kinabalu, Sabah.

Amolops sp. G

Association of these larvae with adults is not possible, though their general similarity to larval *A. phaeomerus* and *A. poecilus* indicates they belong to a member of the *A. jerboa* species group. *Amolops kinabaluensis* cannot be the parental form, as 2 tadpoles in Stage 40 have outer metatarsal tubercles.

DESCRIPTION—**External**—Generally similar to larval *A. phaeomerus*. Head-body width .75–.87 of head-body length, depth .48–.60 of width, eyeball .11–.15 of head-body length (Stages 35–40). Oral disk width .42–.49 of head-body width. Denticles III:3+3 on upper lip, 1+1:IV or 1+1:V on lower. Beaks ribbed, both divided, each half of upper beak with 5–8 coarse serrae, each half of lower with 5–7. Tail length 1.34–1.53 times head-body length, maximum depth .34–.41 of tail length.

Head-body with 4 pairs of glandular clusters; juxtoral cluster with 2–4 glands, prespiracular with 1–4, postocular with 2, posterior midlateral with 3–6. Ventral fin with 1–2 glands (7 larvae in Stages 29–40), 5 (1 in Stage 40), or no glands (2 larvae in Stages 34–35). Snout laterally and area below eye with flattened, brownish protuberances (Stages 34–41); similar structures dorsally on head in half of larvae in same stages; larvae in Stages 29 and 31 without any protuberances. Lateral line pores not visible. Head-body dusky with obscure dark spots; caudal muscle mottled with dark brown; fins dusky.

Head-body length (mm): 9.1, 10.8 (Stages 29, 31), 12.5–14.8 (Stages 34–37), 14.2–15.5 (Stages 39–41). Maximum total length 38.0 mm (Stage 39).

Internal Buccopharyngeal (based on FMNH 109493, Stage 35)—Similar to *A. phaeomerus* except in following characters. Prelingual area of floor smooth except for short, longitudinal, low, thin ridge on each side just before level of tongue anlage; ridge with 2 small peaks or pustules. Tongue anlage rounded in rear. Buccal floor arena with 12 low pustules in a triangular group in each posterolateral third. No other projections from floor. Ventral velum with irregular short, marginal projections medially; 1 short projection laterally. Glottis not open.

Prenarial and narial areas as in *phaeomerus*. Postnarial area with 1 narrow, cylindrical papilla behind median third of each naris; papilla with 2 pustules near tip. Median ridge same size and shape as postnarial papilla. Buccal roof arena with 6–8 very low pustules in posterolateral corners. Glandular zone not visible.

ECOLOGICAL DISTRIBUTION—Information is limited. The single sample came from the same rocky stream as 1 sample (FMNH 109492) of *A. kinabaluensis*.

REFERRED MATERIAL—FMNH 109493, Kaingeran River, near Tambunam, Sabah.

Amolops sp. H

Association with adults poses the same problems as with the three preceding forms. Similarity with larval *A. phaeomerus* and *A. poecilus* places these larvae in the *A. jerboa* species group, but the taxonomic uncertainties surrounding adult forms from western Sabah prevent definite assignment.

DESCRIPTION—**External**—Generally similar to larval *A. phaeomerus*. Head-body width .65–.68 of head-body length, depth .44–.51 of width, eyeball .11–.12 of head-body length (Stages 35–39). Oral disk width .60–.65 of head-body width. Denticles III:3+3 on upper lip, 1+1:IV or 1+1:V on lower. Beaks ribbed, both divided, 5–8 coarse serrae on each half of upper, 4–7 on each half of lower. Tail length 1.40–1.83 times head-body length, maximum depth .23–.29 of tail length.

Head-body with 4 pairs of glandular clusters; juxtoral one with 1–3 glands, prespiracular with 1–2, postocular with 2, posterior midlateral with 2–6. Ventral fin with 3–7 glands. Head-body with conical, pointed protuberances on sides and top of snout and below eye; spinules usually tipped with melanin; tadpoles in Stages 26 and 27 without spinules. Lateral line pores not evident. Head-body and caudal muscle with large dark blotches separated by narrow light areas; fins dusky except adjacent to muscle.

Head-body length (mm): 9.1–10.2 (Stages 26–27), 12.0–13.9 (Stages 35–37), 12.5–15.3 (Stages 38–39). Maximum length 38.33 mm (Stage 38).

Internal Buccopharyngeal (based on FMNH 140213, Stage 36)—Similar to *A. phaeomerus*. Prelingual area of floor smooth except for low, thin, longitudinal ridge on each side just before level of tongue anlage; ridge with 5–7 marginal pustules. Buccal floor arena with 3–4 very short, widely separated papillae in a row on each lateral border; 3 or 4 pustules lateral to last 2 papillae. No other projections from floor of mouth. Ventral velum with irregular, short marginal projections medially; 2 short marginal projections laterally.

Prenarial and narial areas as in *A. phaeomerus*. Postnarial area with 1 cylindrical papilla behind medial third of each naris. Median ridge similar in shape and size to postnarial papilla.

ECOLOGICAL DISTRIBUTION—Information is limited. Both samples were caught in small rocky streams at 90–120 m above sea level.

REFERRED MATERIAL—FMNH 140213, 8 km E. of Tuaran, Sabah; FMNH 141720, Sungei Moyog, 16 km E. of Penampang, Sabah.

RHACOPHORIDAE

Bornean rhacophorid larvae represent five distinct morphological types. The first, and largest, includes the rather generalized larvae of *Polypedates* and most species of *Rhacophorus*. They are homogeneous in general external and buccopharyngeal morphology, though diverse in coloration. Body form is ovoid, robust, and more or less flattened above; the lower lip is margined with 1 or 2 rows of small, homogeneous papillae, rarely interrupted medially; the upper lip has 4 or 5 rows of denticles (rarely 6 or 7), and the lower lip, 3; the width of the oral disk is .33–.50 of the head-body width; there are 2 lingual papillae except for two species with 4; the buccal floor and roof arenas are well defined by lateral papillae, and the interiors have many pustules; the posterior narial wall is drawn out in the medial corner into a short valvular flap; the ventral velum has secretory pits on its dorsal margin. With very few exceptions, all samples have been collected from pools of standing water, either rain-filled depressions on the forest floor or holes in logs and tree trunks.

The robust body form is appropriate to these microhabitats lacking currents.

A second group consists of four larval types, two of which I associate with *Rhacophorus bimaculatus* (Peters) and *R. gauni* (Inger) (see below). These larval forms share a combination of derived features distinguishing them from other groups of ranoid larvae: cuplike oral disks, 3–5 rows of papillae on the lower lip, and denticles decreasing in size from the inner to the outer rows. One of these four larval types occurs in ponded portions of small streams; the other three, in stream microhabitats with distinct currents. As a group, they represent an ecological shift from the *Polypedates-Rhacophorus* group. Liem's (1970) phenogram of *Rhacophorus* species shows *R. bimaculatus* and *R. gauni* forming a species pair within the genus, based on characters of adults. If these larvae are correctly assigned, the gap between these two species and others in *Rhacophorus* is much wider than Liem portrayed.

Larval *Nyctixalus pictus,* found only in tree holes and similar containers, is flatter than typical rhacophorid tadpoles and has an almost circular outline, particularly in early stages. The serrae of its beaks are fine and long. Although it has 3 gill chambers, the inner one is much reduced. Two other larval forms diverge even further from the typical rhacophorid structural plan. One of them, which cannot be assigned to genus, has a terminal rather than ventral oral disk, scalloped rather than papillate lips, and only a single, widely interrupted row of denticles. The second highly modified form is larval *Philautus hosei,* which lacks an operculum and the usual external oral structures and apparently has an abbreviated swimming stage, if any.

These larval *Nyctixalus* and *Philautus* depart sufficiently from other known larval rhacophorids to buttress the definitions of these genera based on adult morphology (Liem, 1970). That this is the case for *Philautus* has been known for some time (e.g., Dring, 1979). The unassigned larval form resembles the tree-hole tadpole from Thailand described by Wassersug et al. (1981). They suggest the existence of an as yet undefined rhacophorid genus. Unfortunately, neither of these forms can be assigned to species of adults at this time.

Larval *Polypedates* and *Rhacophorus* described below provide little support for the separation of these genera. Larval *P. macrotis* and *P. otilophus* differ from all the others in having eyes laterally situated (optic capsules visible from below) and deeper tails (about half the length of the tail). Larval *P. colletti,* however, is more like larval *Rhacophorus* in these characters.

Polypedates

Larval *P. macrotis* is used as the standard against which the other two forms are compared.

Polypedates macrotis (Boulenger)

Association of these larvae with *P. macrotis* is based upon several complete developmental series reared from nests or from tadpoles caught at pools around which amplecant pairs and calling males were observed. Juveniles in late metamorphic stages (44–45) have a rudiment of web between the 2 inner fingers and webbing between the toes as in adult *macrotis.* For illustrations of this larval form, see Inger (1966, figs. 62–63).

DESCRIPTION—**External**—Head-body oval, snout broadly rounded, body flattened above except at the root of the tail, rounded below; maximum width near center of body, .57–.67 of head-body length, depth (excluding raised root of tail) .83–.97 of head-body width; eyes lateral, visible from below, eyeball .09–.13 of head-body length (Stages 27–39); interorbital more than three times diameter of eyeball, .60–.66 of head-body width, greater than eye–snout distance; nostrils lateral, open, rim not raised; internarial half to two-thirds of interorbital; nasolacrimal duct visible. Oral disk ventral, subterminal, width .38–.44 of head-body width; short, thick papillae in crowded single row across lower lip, with narrow median gap equal to width of 3–5 papillae; similar papillae at corners of upper lip; denticles I:4+4/1+1:II; beaks finely serrated, black in marginal two-thirds, upper with weak median convexity. Spiracle sinistral, low on side, tube fused to body wall; opening wide, snout–spiracle .48–.58 of head-body length. Anal tube dextral. Tail with margins convex, tapering gradually in distal third to narrow tip; tail length 1.2–1.7 of head-body length, maximum depth .44–.55 of tail length; origin of dorsal fin over end of body, deeper than ventral fin only in distal half; both fins deeper than caudal muscle except at base; both fins with thickened areas proximally near muscle. No glands or lateral line pores visible.

Color in life of head-body dark green with scattered light flecks dorsally and laterally, below silvery gray; caudal muscle with dark reticulation proximally; thickened area of dorsal fin dark green, that of ventral fin white with small black dots; rest of fins with scattered melanophores.

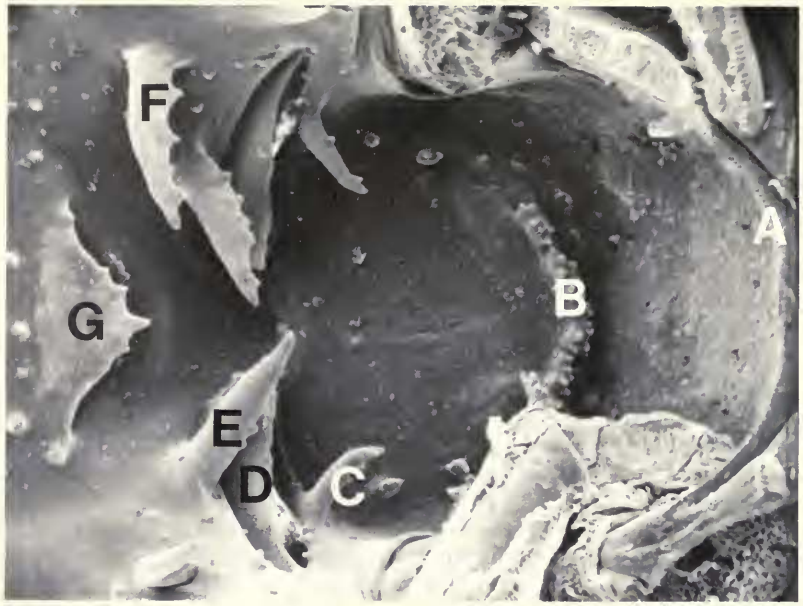

FIG. 35. *Polypedates macrotis.* Anterior portion of buccal roof (× 42), anterior to right. **A,** Beak; **B,** prenarial ridge; **C,** papilla of anterior narial wall; **D,** posterior narial wall; **E,** postnarial papilla; **F,** lateral ridge papilla; **G,** median ridge.

The denticles are angled toward the mouth, rounded in outline, concave on the adoral surface, and with 12–15 long, triangular cusps around the distal two-thirds of the margin. They are very similar to those of *Polypedates otilophus.*

Head-body lengths (mm): 9.6–15.0 (Stages 26–27), 15.0 (Stage 30), 14.7–15.5 (Stages 34–37), 16.2–18.0 (Stages 39–40). Total length to 47.0 (Stage 37).

Internal Buccopharyngeal (based on FMNH 63546, Stage 38)—Prelingual area of floor with 1 cylindrical papilla laterally on each side; gap between papillae about twice height of papillae, equal to distance from papilla to tongue anlage; no other papillae or pustules in prelingual area. Tongue anlage longer than wide; 2 simple lingual papillae in center. Buccal floor arena with 6–10 slender, pointed papillae along posterolateral boundary on each side; first papilla on each side with a few pustules, others smooth; rear half of interior with about 30 low pustules; anterior half of floor arena smooth. Buccal pockets oval, wide; 1 short papilla anterior to pocket. Ventral velum supported by spicules; margin with 7 projections, lateral ones more widely spaced; no median notch; projections and margin with secretory pits. Glottis behind velum. Branchial baskets with 3 gill chambers; median wall of middle chamber with 9 filter rows; filter canals open.

Prenarial area of roof (fig. 35) with short, arched, pustulose, transverse ridge in center; 3 short papillae or pustules extend ridge laterally on each side. Nares transverse, distance between them less than length of one; anterior narial wall low, pustulose, a conical, pustulose papilla rising from its center; posterior wall taller, valvular, expanded in medial corner. Postnarial area with 1 or 2 pustules laterally; a tall, thick, tapering, medially curved papilla posterior to median corner of naris, papilla pustulose on anterior face; a low, pustulose, transverse ridge anterior to median ridge. Lateral ridge papilla tapering, pustulose, equal in height to postnarial papilla. Median ridge a low triangle; height about half width; margin with a few pustules. Buccal roof arena with 4–5 papillae forming middle of each lateral border; interior of arena with about 60 well-spaced pustules; 2 short papillae far laterally. Glandular zone extending across roof. Margin of dorsal velum ragged.

ECOLOGICAL DISTRIBUTION—Limited to pools of standing water away from streams. Seven samples were taken from pools in the ground at the edge of forest, and 1, from a pool in a large stump. Of the 7 samples, 2 were taken with larval *P. otilophus* and 1 with larval *Rhacophorus pardalis.*

REFERRED MATERIAL—FMNH 63546, 63549–53, 63555, Bukit Kretam, Sandakan District, Sabah; FMNH 77541–2, 120212, Kalabakan, Tawau

District, Sabah; FMNH 83028, Long Seniai, Akah River, Fourth Division, Sarawak.

Polypedates colletti (Boulenger)

Association of these larvae with adult *P. colletti* is based on features of metamorphic stages (42 and 44) in series reared in field laboratories. These individuals lack webbing on the hand, which separates them from all Bornean *Rhacophorus.* They have less than full webbing (about two-thirds) on the toes and lack rows of tubercles or flaps of skin on the outer margin of the hind limb. As they also have typical rhacophorid digital disks, identification seems limited to *P. colletti, P. macrotis, P. otilophus,* and *P. leucomystax.* The three last can be eliminated because their larvae, which are known (see Inger, 1966, and this paper), differ from these tadpoles in having a median gap in the papillae of the lower lip, the origin of the dorsal fin over the end of the body, and the eyes far enough lateral to be visible from below. Thus, *P. colletti,* the only other member of the genus known from Borneo, remains as the likely parent.

Two factors leave the identification uncertain. First, the metamorphic individuals show no sign of the small conical tubercle present at the heel in adult *P. colletti.* Secondly, the samples from Sarawak are slightly different from the 2 from eastern Sabah. Although all these samples are alike in the features that distinguish them from the other larvae of *Polypedates* (see above), the Sarawak tadpoles have shorter and deeper tails and have a semilunar, silvery reflecting patch just behind the oral disk, which is not evident in the others. Provisionally, all these differences are interpreted as intraspecific, geographic variation. There remains the possibility that another species of *Polypedates,* adults of which have not yet been collected, is the parental species of one of these types of larvae.

DESCRIPTION—**External**—Body not as robust as that of larval *P. macrotis.* Head-body width .65–.68 of head-body length, depth .70–.82 of width; eyeball .11–.13 of head-body length (Stages 26–38); interorbital .31–.36 of head-body width; width of oral disk .39–.48 of head-body width; snout–spiracle .56–.63 of head-body length. Eyes dorsolateral, not visible from below; interorbital about twice eye diameter; papillae of lower lip without median interruption; denticles I:3+3/1+1:II (Stages 26–31) or I:4+4/III (Stages 31–38); beaks black on margins, upper with weak median convexity.

Tail shape and size varying geographically: in Sarawak larvae dorsal margins distinctly convex, tip broadly rounded, length 1.5–1.9 of head-body length, depth .37–.44 of tail length; in Sabah larvae dorsal margin almost straight, tip narrow, length 1.8–2.3 of head-body length, depth .23–.27 of tail length. In all samples origin of dorsal fin at end of body.

In preservative general coloration pale yellowish; head-body with broad dark band across body; usually a faint dark spot on side of snout; caudal muscle and dorsal fin with small dark spots. In life Sabah tadpoles translucent, green flecks on body, black reticulation on caudal muscle and dorsal fin.

Head-body lengths (mm): 5.8–6.5 (Stages 26–28), 7.1–7.8 (Stages 31–32), 7.5–8.8 (Stages 36–37), 7.9–8.6 (Stages 38–42). Total length to 26.3 mm (Stage 37).

Internal Buccopharyngeal (based on FMNH 157735, Stage 36)—Prelingual area of floor with 4 papillae in a transverse series across posterior border; median pair short, conical, separated by more than their height; lateral ones very tall, flattened, concave forward, with 3 branches in apical half, branches with short projections on anterior surfaces; a bifurcate, pustulose papilla anterior to lateral papilla and about half latter's height. Tongue anlage weakly elevated; 2 tall, slender lingual papillae in center, well separated. Buccal floor arena oval; 5 tall, curved papillae in a row in posterior half of each lateral border; 1 short papilla lateral to first tall one and a pair of short ones posterolateral from fourth; ca. 50 evenly spaced pustules in posterior two-thirds of interior of arena. Buccal pocket transverse, curved. Ventral velum supported by spicules; no median notch; margin with 10 short projections, lateral ones widely spaced; margin and projections with secretory pits. Glottis behind velum. Branchial baskets almost fully exposed; 3 gill chambers, slightly oblique; filter ruffles with tertiary folds; 10 or 11 filter rows on median wall of middle gill chamber; filter canals open.

Prenarial area of roof with transverse, forwardly arched, crenulate ridge near center. Nares transverse, oval, separated by two-thirds length of one; anterior narial wall thick, raised, pustulose; a medially curved, pustulose papilla rising from middle of anterior wall; posterior wall taller, thin, smooth, a rounded valvular expansion in medial corner. Postnarial area with a depression behind each naris; a tall, medially curved papilla from middle of margin of depression, papilla pustulose on anterior face, meeting corresponding papilla of other side; a transverse row of low papillae or pustules just

TABLE 21. Microhabitat distribution of larval *Polypedates colletti* in forest streams and their occurrence with tadpoles of other species.

Species	No. of samples		
	Protected side pool	Pothole on bank	Pool of intermittent stream
Leptobrachium nigrops	1	...	...
Microhyla petrigena	...	1	...
Rana blythi	11	...	...
Rana ibanorum	...	1	...
Rana ingeri	...	2	...
Rana kuhli	1	...	...
Rana palavanensis	...	...	1
Without other tadpoles	0	0	2
Total samples	1	2	3

before median ridge. Lateral ridge papilla flattened laterally; apical third divided into 1 long, slender anterior branch and 2 shorter posterior ones having a common base; anterior margin with 2 or 3 pustules. Median ridge triangular, base twice height, margin with 5 pustules. Buccal roof arena rectangular; 3 tall, simple papillae in a row on each lateral border; interior with ca. 75 evenly spaced pustules. Glandular zone deep, continuous across roof. Dorsal velum with 1 or 2 short projections in median third.

ECOLOGICAL DISTRIBUTION—Limited to microhabitats with very weak or no current, where larval *P. colletti* was found with a variety of other tadpoles (table 21). This is the only larval rhacophorid found exclusively in stream or streamside environments.

REFERRED MATERIAL—FMNH 63513, 213633–6, Bukit Kretam, Sandakan District, Sabah; FMNH 157734–5, 157988, Sungei Pesu, Tubau district, Fourth Division, Sarawak; FMNH 195607, 214704–5, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Polypedates otilophus (Boulenger)

Association of larvae with adults is based upon developmental series reared in the field laboratory. These samples agree with those described and assigned to *P. otilophus* by Boulenger (1893). In early metamorphic stages, the tadpole acquires longitudinal lines on the back and numerous narrow crossbars on the hind leg characteristic of adult *P. otilophus.*

DESCRIPTION—**External**—General form of body and tail as in larval *P. macrotis,* though body bulkier (see Inger, 1966, fig. 65). Head-body width .58–.74 of head-body length, depth .86–1.0 of width; eyeball .08–.11 of head-body length (Stages 26–37); interorbital .57–.74 of head-body width; width of oral disk .32–.41 of head-body width; snout–spiracle .48–.59 of head-body length; tail length 1.2–1.5 of head-body length, maximum depth .42–.51 of tail length. Eyes lateral as in *macrotis*; papillae in double staggered row on lower lip, with median interruption; denticles I:3+3/III (Stages 26–27), I:4+4/III (Stages 30 onward); beaks heavy, black over most of depth, finely serrated, upper with strong median convexity (see Inger, 1966, fig. 65). Both fins with thickened areas proximally near caudal muscle. Lateral line pores in a pair of rows, 1 above nostril and eye to end of body, 1 below nostril and eye; 1 row midlaterally on caudal muscle.

Color in life yellowish green above, silvery white below; dorsal fin with golden flecks. In preservative color fading to straw yellow; no markings on body or tail.

Head-body lengths (mm): 12.3–20.0 (Stages 26–27), 17.8–27.5 (Stages 36–37). Total length to 62.5 mm (Stage 37).

Internal Buccopharyngeal (based on FMNH 83027, Stage 35, FMNH 120211, Stage 36, and FMNH 63544, Stage 27, last examined by means of SEM)—Prelingual area of floor (fig. 36) with 3 pustulose papillae along each lateral border; middle one tallest; 2–4 short pustulose papillae in transverse line between last lateral papillae, forming rear boundary of area. Tongue anlage distinct, low, width equal to length; 4 lingual papillae in center anteriorly, 2 median ones tallest, equal to or taller than tallest prelingual papillae. Buccal floor arena (fig. 36) with 6–9 papillae in staggered row, forming incomplete lateral border; a few pustules surrounding first papilla; interior with pustules evenly scattered throughout or concentrated in rear half. Buccal pockets wide, transverse. Ventral velum supported by spicules; no median notch; 5–8 short marginal projections on each side, median ones closer together; projections and margin of velum with secretory pits. Glottis behind velum. Branchial baskets with 3 chambers; median wall of middle chamber with 9 filter rows; filter ruffles tall, with tertiary folds; filter canals narrow but open.

Prenarial area of roof with anteriorly arched, low, pustulose ridge midway between beak and nares; 2–4 short papillae extend ridge laterally. Nares transversely oval, long, gap between them about half length of one; anterior narial wall low,

FIG. 36. *Polypedates otilophus.* Floor of buccopharyngeal cavity (× 20), anterior at right. **A,** Beak; **B,** lingual papilla; **C,** buccal floor arena; **D,** lateral papilla of buccal floor arena; **E,** ventral velum; **F,** branchial basket.

with tall, medially curved, pustulose papilla laterally; posterior wall higher, thin, with rounded, valvular medial expansion curving around onto anterior wall. Postnarial area with a groove behind narial wall followed by a tall, pustulose, slightly curved papilla behind middle of naris; a short papilla behind lateral third of naris; a short transverse ridge with 2 short peaks in front of median ridge. Lateral ridge papilla slender, pustulose, not as tall or as thick as larger postnarial papilla; adjacent to lateral postnarial papilla. Median ridge wide, low, with 4 short marginal peaks. Buccal roof arena with 3–5 slender, pustulose papillae in a row in middle of each lateral border; interior with 25–50 evenly scattered low papillae or pustules. FMNH 63544 with a cluster of 10 pustules at lateral edge of roof at level of roof arena papillae. FMNH 120211 with 3 or 4 papillae in extreme posterolateral corner of roof. Glandular zone deep, extending full width of roof. Dorsal velum with about 12 low, rounded projections on each side.

ECOLOGICAL DISTRIBUTION—Larval *P. otilophus* appears to be limited to pools of water away from streams. All 6 samples for which data are available were taken in such pools at the edge of forest clearings. Two included larval *P. macrotis,* a third, larval *Rhacophorus pardalis,* and a fourth, tadpoles of *Rana nicobariensis.*

REFERRED MATERIAL—FMNH 63544, 63548, 63554, Bukit Kretam, Sandakan District, Sabah; FMNH 77538–40, 120211, Kalabakan, Tawau District, Sabah; FMNH 83027, Long Akah, Akah River, Fourth Division, Sarawak.

Rhacophorus

As already noted (p. 69) larvae of this genus constitute two distinct clusters. The first consists of larvae of species that are typical members of this genus, e.g., *pardalis* and *nigropalmatus.* As a group, they are unusual among Bornean tadpoles for the amount of interspecific differentiation in color pattern. Larvae of *R. dulitensis,* for example, have a uniformly grayish body but a distinctly bicolored tail, whereas tadpoles of *R. pardalis* often have spotted bodies, and those of *R. nigopalma-*

tus, spotted tails. Larval *R. harrissoni* are unmarked. In other respects they are generally similar to one another. Larval *R. nigropalmatus* are used as the standard form to which other members of this group are compared. They are presented first in the species accounts that follow.

The second group consists of four larval forms distinguished from the first by their specialized oral disks (see above, p. 69). Although assignment is tentative, I associate these larvae with *Rhacophorus bimaculatus* (Peters) and related species. They are discussed in greater detail below (p. 81).

Rhacophorus nigropalmatus Boulenger

Association with adult *nigropalmatus* is based on developmental series extending from limb bud to metamorphosis. The most advanced individual, which has only a stub of tail remaining, has the very large hands, fully webbed toes and outer fingers, and smooth flaps of skin on the edges of fore and hind limbs characteristic of *R. nigropalmatus.* The webbing of the inner fingers is not as extensive as that in adults.

DESCRIPTION—**External**—Head-body oval, snout rounded, body slightly flattened above and below, maximum width midway between eyes and end of body, .65–.71 of head-body length, depth .67–.78 of width; eyes dorsolateral, not visible from below, eyeball .09–.12 of head-body length (Stages 36–41); interorbital .33–.37 of head-body width, twice diameter of eyeball, slightly greater than eye–snout distance; nostrils dorsolateral, open, rim not raised, internarial about two-thirds of interorbital; nasolacrimal duct visible from Stage 36 onward. Oral disk ventral, subterminal, width .34–.39 of head-body width; short, thick papillae in double staggered row across lower lip, usually without gap in center; papillae at corners of upper lip; denticles I:4+4/1+1:II, rarely with 3 or 5 divided rows on upper lip; beaks finely serrated, black in marginal third, upper without median convexity. Spiracle sinistral, low on side, tube fused to body wall, snout–spiracle .51–.61 of head-body length. Anal tube dextral, fused to ventral fin, opening halfway to fin margin. Tail weakly convex, tapering near end to narrow, rounded tip; tail length 1.4–1.9 times head-body length, maximum depth .31–.39 of tail length; caudal muscle deeper than either fin in proximal three-fifths; origin of dorsal at end of body, slightly deeper than ventral except near end.

Color in life of head-body pale gray above, white below; tail gray with black spots on muscle and fins; margin of dorsal fin and usually that of ventral dark.

Head-body lengths (mm): 9.3–14.3 (Stages 26–29), 12.2–13.8 (Stage 31), 13.9–14.8 (Stage 36), 13.7–15.8 (Stages 38–41). Total length to 50 mm (Stage 39). With few exceptions, these are measurements of animals reared 5–35 days.

Internal Buccopharyngeal (based on FMNH 137917, Stage 39)—Prelingual area of floor bounded posteriorly by 4 large papillae in slightly arched transverse row; median pair with anteromedian edge pustulose; lateral papillae pustulose on all sides, 2 short branches at tip; a transverse row of 6 short pustulose papillae across middle of prelingual. Tongue anlage distinct, oval, with small tip at rear; 4 lingual papillae in transverse row across center of tongue anlage, bases of papillae touching, median 2 larger. Buccal floor arena hexagonal, with 11 or 12 tall papillae in irregular double row on each side forming lateral and posterior borders; a deep, median longitudinal groove in anterior two-thirds of arena; about 50 low pustules scattered across rear half of arena and onto dorsal surface of velum; a group of low pustules and several short, conical papillae in anterolateral corners of arena. Buccal pockets wide, transverse, perforation not evident. Ventral velum supported by spicules; no median notch; 6 marginal projections on each side, the lateral 3 longest and more widely spaced; margin and projections with secretory pits. Glottis in raised disk behind velum. Branchial baskets largely exposed; 3 gill chambers slightly oblique; filter ruffles with tertiary folds; 12 filter rows on median wall of middle chamber; filter canals narrow.

Prenarial area of roof with forwardly arched, transverse, pustulose ridge across middle. Nares transverse, elongate, gap between them about two-thirds length of one; anterior narial wall thick, pustulose, with tall, medially curved, pustulose papilla rising from center; posterior narial wall thin, smooth, low laterally, with rounded, valvular expansion medially. Postnarial area with shallow groove behind naris; a tall, medially curved, pustulose papilla behind medial corner of naris, postnarial papilla taller than narial papilla; 2 low pustules medially in front of median ridge. Lateral ridge papilla pointed, curved posteriorly, a few pustules on its anterior margin. Median ridge rounded, narrowed above base, height about equal to width. Buccal roof arena with 5 conical papillae in a curved row in center of each lateral border; about 100 low, evenly spaced pustules occupying

interior. Glandular zone deep, extending across roof. Dorsal velum damaged.

ECOLOGICAL DISTRIBUTION—Larval *R. nigropalmatus* is limited to small pools on the forest floor. At Nanga Tekalit, Sarawak, 2 samples were taken in pig wallows with larval *Microhyla* sp. C. At Kalabakan, Sabah, 2 samples were obtained from rain-filled depressions at the edge of forest. One of these also contained larval *Rana chalconota.*

REFERRED MATERIAL—FMNH 77544, 77548, Kalabakan, Tawau District, Sabah; FMNH 137912–5, 137917–20, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Rhacophorus appendiculatus (Günther)

Association of these larvae with *appendiculatus* is not certain and has been based on webbing of the hand and foot and presence of light areas at elbows and heels (Inger, 1966). However, in those respects they also resemble *Rhacophorus bimaculatus* (Peters). In metamorphic stages they lack dermal fringes along arms and legs characteristic of *R. appendiculatus.* The microhabitats in which they were found, rain pools removed from streams, are the kinds of situations around which adult *appendiculatus* were also caught. Adult *R. bimaculatus,* on the other hand, were caught only along stream banks.

DESCRIPTION—**External**—General form as in larval *R. nigropalmatus,* though smaller and tail with more drawn-out tip. Head-body width .62–.67 of head-body length, depth .64–.74 of width; eyeball .11–.13 of head-body length (Stages 36–41); interorbital .29–.34 of head-body width; width of oral disk .43–.44 of head-body width; snout–spiracle .57–.65 of head-body length; tail length 1.5–2.0 times head-body length, maximum depth .46–.54 of tail length. Interorbital less than twice eye diameter; papillae of lower lip without median gap; denticles I:3+3 or I:4+4 on upper lip, 1+1:II on lower; beaks as in *nigropalmatus.*

In preservative head-body brown dorsally and laterally, with faint light areas at rear, ventrally whitish; caudal muscle brown with light, irregular spots dorsally; dorsal fin dusky throughout, ventral fin dusky near tip.

Head-body lengths (mm): 6.8–7.8 (Stages 36–37), 8.8–9.2 (Stages 40–41). Total length to 25.9 mm (Stage 41).

ECOLOGICAL DISTRIBUTION—Appears to be confined to rain pools on the forest floor. One of the 2 samples was found with larval *Microhyla perparva.*

REFERRED MATERIAL—FMNH 146252–5, Labang, Kemena River, Fourth Division, Sarawak; FMNH 216173, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Rhacophorus dulitensis Boulenger

Association of these larvae with adults of *R. dulitensis* is based upon developmental series in which metamorphosing young (Stage 42) have webbing of feet and hands as in *dulitensis* and the diagnostic transverse supra-anal fold.

DESCRIPTION—**External**—Similar to larval *R. nigropalmatus* in general form of head-body, oral disk, and tail. Head-body width .62–.66 of head-body length, depth .72–.79 of width; eyeball .09–.10 of head-body length (Stages 28–36); interorbital .34–.39 of head-body width; width of oral disk .43–.49 of head-body width; snout–spiracle .53–.56 of head-body length; tail length 1.3–1.8 times head-body length, maximum depth .34–.40 of tail length. Interorbital more than twice diameter of eyeball; papillae in continuous double row across lower lip; denticles I:5+5/1+1:II; beaks as in *nigropalmatus.*

Color in life of head-body and anterior half of tail pale grayish brown; a black vertical wavy line in middle of tail beyond which tail is darker; underside of head-body whitish.

Head-body lengths (mm): 13.2–15.8 (Stage 28), 15.0 (Stages 31–32), 15.0–16.3 (Stages 34–36), 14.2–15.8 (Stages 38–42). Total lengths to 42.7 mm (Stage 35).

The denticles are densely crowded in rows, with a curved, spatulate shaft. The distal two-thirds of the shaft has 12–14 closely spaced, thick tines.

Internal Buccopharyngeal (based on FMNH 139374, Stage 35, and SEM examination of FMNH 137950, Stage 36)—Prelingual area of floor with 4 long papillae in transverse row across rear, lateral ones thicker, longer, and slightly curved posterolaterad; all 4 pustulose along anterior margins and at tips; a pair of short pustulose papillae on each side anterolaterad from large lateral ones. Tongue anlage raised, as wide as long; 2 lingual papillae in center. Buccal floor arena poorly defined; on each side 1 short papilla anterolaterally followed by a large flattened papilla mesad from buccal pocket; 3–4 conical papillae in posterolateral corner of arena; interior smooth anteriorly, with 10–12 short papillae and 6 low pustules. Buccal pocket

a narrow arc; 2 prepocket pustules. Ventral velum deep, supported by spicules; no median notch; margin with 14 finger-like projections, 3 lateralmost on each side longer and more widely spaced than remainder; margin and projections with secretory pits. Glottis behind velum. Branchial baskets with 3 chambers; filter ruffles with tertiary folds; median wall of middle chamber with 12 filter rows; filter canals open.

Prenarial area of roof with forwardly arched, pustulose transverse ridge. Nares transverse, narrow, gap between nares less than half length of one; anterior narial wall thick, low, with several small pustules and a tall, medially curved, pustulose papilla rising from its center; posterior wall thin, valvular, smooth, with a wide, tall expansion medially. Postnarial area with a deep groove immediately behind narial wall; a tall, thick, medially curved, pustulose papilla rising from rear wall of groove directly behind expanded portion of narial wall, almost long enough to meet corresponding papilla from other side; about 12 low pustules scattered across postnarial area. Lateral ridge papilla pustulose, not as tall or as thick as postnarial papilla. Median ridge semilunar or truncate, width about twice height. Buccal roof arena with 4 conical papillae in middle of each lateral border; anterior half of interior with 30–40 low pustules, rest of interior smooth. Glandular zone deep, extending across roof. Dorsal velum with 3 or 4 short projections medially, margin with pustules laterally.

Ecological Distribution—Larval *R. dulitensis* appears to be limited to forest floor pools removed from streams. All 4 samples were obtained in pig wallows. One sample included larval *Microhyla borneensis* and *Rana luctuosa,* and a second, the same two kinds of larvae plus larval *Microhyla* sp. C.

Referred Material—FMNH 137949–51, 137973–4, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Rhacophorus harrissoni Inger and Haile

Association of these larvae with *R. harrissoni* is based upon complete developmental series from hatchlings to metamorphosing young (Stage 43). The last agree with adult *harrissoni* in having fully webbed outer fingers, dark crossbars on the limbs, but no dermal fringes on lower arm, tarsus, or above the anus. As noted earlier (Inger, 1966), these features do not distinguish them from *R. fasciatus.* However, *R. harrissoni* was a relatively common species at the three localities from which we collected larvae, whereas only a single adult *fasciatus* was caught.

Description—**External**—Generally similar to larval *R. nigropalmatus,* but tail not as deep. Head-body width .60–.74 of head-body length, depth .74–.86 of width; eyeball .10–.11 of head-body length (Stages 26–27), .14–.15 (Stages 37–41); interorbital .36–.42 of head-body width; width of oral disk .33–.41 of head-body width; snout–spiracle .58–.64 of head-body length; tail length 1.9–2.2 times head-body length, maximum depth .25–.32 of tail length. Interorbital twice eye diameter; no gap in papillae of lower lip; denticles I:3+3 (7 individuals) or I:4+4 (3) on upper lip, III on lower.

Color in life of head-body and tail dark gray.

Head-body lengths (mm): 9.6–10.0 (Stages 26–27), 9.5–10.8 (Stages 30–31), 10.6–13.0 (Stages 39–41). Total length to 41.3 mm (Stage 41).

The denticles are spatulate, with the margins of the shaft curved toward the mouth. There are 20–22 wide cusps on the apical two-thirds of the shaft.

Internal Buccopharyngeal (based on FMNH 157665, Stages 37–38, latter examined by means of SEM)—Prelingual area of floor bounded posteriorly by 4 papillae; median pair small, conical, pustulose; lateral ones large, thick, flattened, each divided into 2 major branches bearing short marginal projections; anterior to posterolateral papilla a large subcylindrical papilla with small marginal projections near its tip; 3 or 4 small pustules anteromedially. Tongue anlage conspicuous, longer than wide; 2 lingual papillae close together near center. Buccal floor arena oval, 7–9 papillae in a staggered row on each lateral border; largest papillae in center of row, pustulose at tips; 5–7 short, pointed papillae laterad from first 2 papillae; interior of arena with 6–9 low pustules in posterior half. Buccal pockets wide, oblique, not perforated; a single pointed papilla at anteromedian corner of pocket. Ventral velum supported by spicules; no median notch; margin with 6 short projections on each side; margin and projections with secretory pits. Glottis behind velum. Branchial baskets with 3 gill chambers; filter ruffles with tertiary folds; median wall of middle chamber with 9 filter rows; filter canals narrowed but open.

Prenarial area of roof with forwardly arched, crenulate, transverse ridge; pustulose near center. Nares transverse, oval, distance between them about two-thirds length of one; anterior narial wall raised, pustulose, a tall, pustulose papilla rising from lateral third; posterior narial wall thin, smooth, about same depth as anterior (fig. 37).

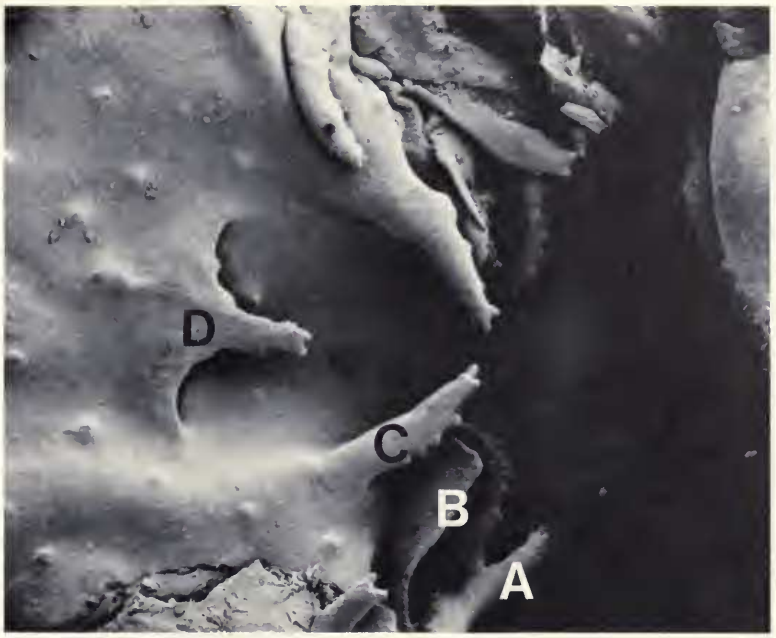

FIG. 37. *Rhacophorus harrissoni.* Narial region of buccal roof (× 72), anterior to right. **A,** Papilla of anterior narial wall; **B,** posterior narial wall; **C,** postnarial papilla; **D,** median ridge.

Postnarial area with depression behind each naris; a tall, pointed, pustulose papilla behind median corner of depression, projecting anteromesad; a short papilla behind lateral corner of depression; several low pustules medially. Lateral ridge papilla conical, pustulose, not as tall as medial postnarial papilla. Median ridge with wide base, shape triangular or attenuate, margin with 4–7 low pustules. Buccal roof arena with 3 tall and 2 short, pointed papillae in double row near middle of each lateral border; interior of arena with about 40 low, evenly spaced pustules. Glandular zone deep, extending across roof. Dorsal velum damaged in dissections.

ECOLOGICAL DISTRIBUTION—Restricted to tree holes. Six samples were taken from water tanks formed by anastomosing buttresses, 5 from holes in trunks, and 2 from holes in large surface roots. The root holes were only 15 cm above the ground. The other containers were .75–3.6 m high, and their surfaces, 8 × 10 to 30 × 50 cm. No tadpoles of other species were found in these containers.

REFERRED MATERIAL—BMNH 1978.299–300, Mt. Mulu National Park, Fourth Division, Sarawak; FMNH 157658–63, Labang, Kemena River, Fourth Division, Sarawak; FMNH 157664–5, Sungei Pesu, Tubau district, Fourth Division, Sarawak; FMNH 214706–16, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Rhacophorus pardalis Günther

Association of these larvae with adults of *R. pardalis* is based on a complete developmental series, culminating in a metamorphosing individual (Stage 42) having fully webbed outer fingers, smooth ridges of skin along the outer edge of forearm and lower leg, and a smooth, rounded ridge at the heel. There is no supra-anal ridge. Although the dermal appendages of the limb are not as wide as those in adults, this difference is consistent within the genus *Rhacophorus*; transforming young usually do not have dermal flaps or fringes as well developed as those in adults.

DESCRIPTION—**External**—Similar to larval *R. nigropalmatus* in general form. Head-body width .60–.71 of head-body length, depth .72–.83 of width; eyeball .10–.12 of head-body length (Stages 31–38); interorbital .33–.39 of head-body width; width of oral disk .40–.49 of head-body width; snout–spiracle .47–.61 of head-body length; tail length 1.7–1.9 times head-body length, maximum depth .28–.38 of tail length. Interorbital twice diameter of eyeball; papillae in continuous double

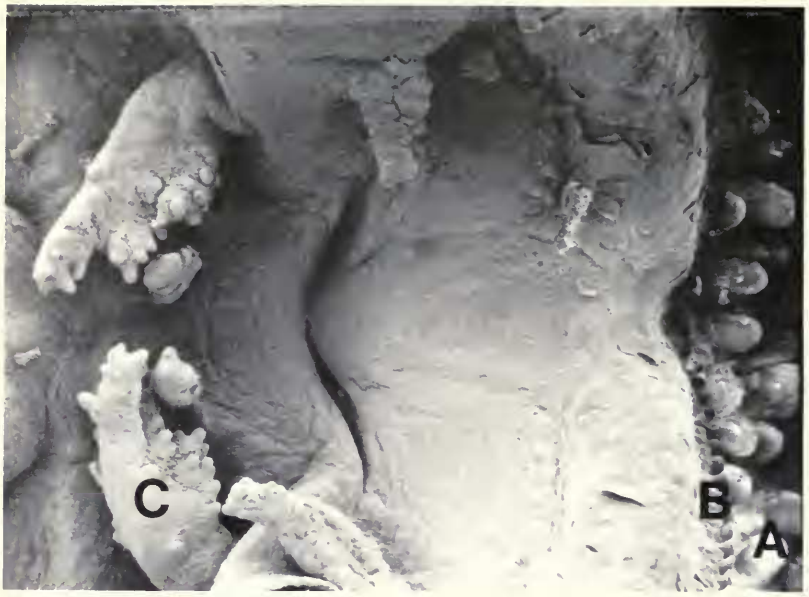

FIG. 38. *Rhacophorus pardalis.* Prelingual portion of buccal floor (× 110), anterior to right. **A,** Labial papillae; **B,** beak; **C,** prelingual palp.

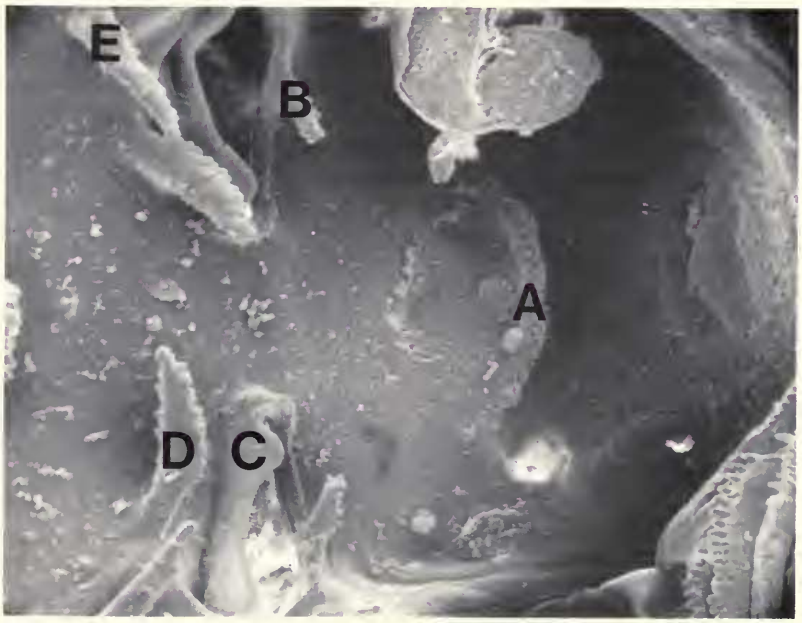

FIG. 39. *Rhacophorus pardalis.* Narial region of buccal roof (× 50), anterior to right. **A,** Prenarial ridge; **B,** papilla of anterior narial wall; **C,** posterior narial wall; **D,** postnarial papilla; **E,** lateral ridge papilla.

row across lower lip; denticles II:4+4 or II:5+5 on upper lip, III on lower.

Color variable; Sabah larvae usually with distinct dark spots on head-body; Sarawak larvae usually unspotted or with one spot on side of snout.

Head-body lengths (mm): 5.8–6.3 (Stages 26–27), 9.8–13.1 (Stages 30–31), 11.3–15.0 (Stages 36–37). Total length to 43.2 mm (Stage 37).

The denticles are closely packed in rows, spatulate in outline, with a truncate apex. The distal

half of the shaft has 12–14 short, triangular cusps.

Internal Buccopharyngeal (based on FMNH 83026, Stage 36, and SEM examination of FMNH 140242, Stage 37)—Prelingual area of floor (fig. 38) with a large, flattened palp in each posterolateral corner and 2 short, thick pustulose papillae between them; large palps with 3 short branches, anteromedial surfaces pustulose; a thick, pustulose papilla anterior to each palp; a transverse row of low pustules in anterior third of prelingual. Tongue anlage distinct, oval, truncate anteriorly, rounded in rear; 2 short papillae close together in center. Buccal floor arena with 6–8 tall, flattened, branched or pustulose papillae in a staggered row in each lateral border; interior of arena smooth anteriorly, with about 15 widely separated, low pustules in posterior third; a patch of about 25 pustules anterior and lateral to first papillae. Buccal pockets narrow, slightly oblique, length greater than width of buccal floor arena; perforation not evident. Ventral velum supported by spicules; no median notch; margin with 8 or 9 thick projections on each side, 1 or 2 of median ones branched; margin and projections with secretory pits. Glottis behind velum. Branchial baskets largely exposed; 3 gill chambers slightly oblique; filter ruffles with tertiary folds; 9 filter rows on median wall of middle chamber; filter canals wide.

Prenarial area of roof with forwardly arched, pustulose, transverse ridge in center. Nares transverse, oval, gap between them about half length of one; anterior narial wall raised, thin, margin with weak pustules; a short curved, pustulose papilla rising from center; posterior narial wall thin, smooth, with rounded, valvular expansion medially (fig. 39). Postnarial area with depression behind each naris; a tall, medially curved, pustulose papilla behind middle of each depression. Lateral ridge papilla slender, pustulose, not as tall as postnarial papilla. Median ridge wide, triangular, with weakly pustulose margin. Buccal roof arena with 4–6 papillae in curved row on each lateral border; evenly spaced pustules throughout interior of arena, some behind level of last lateral papillae. In FMNH 83026, 3 short, pointed papillae in extreme lateral portion of roof opposite center of and widely separated from arena. Glandular zone deep, continuous across roof. Dorsal velum with 5–8 low undulations or projections.

Ecological Distribution—Restricted to microhabitats of no or little current. Four samples were obtained in rain pools at some distance from streams, 1 from a pool of a small intermittent stream, and 3 from potholes or other pools in floodplains of small streams. Adults were observed in breeding aggregations at seepages near the banks of streams and around rain pools. One of the pothole samples also included larval *Microhyla petrigena,* and a second one, larvae of *M. petrigena, Bufo divergens,* and *Rana ibanorum.* The sample from the intermittent stream included larval *Polypedates otilophus,* and 1 from a rain pool, larval *P. macrotis.*

Referred Material—FMNH 63542–3, 63545, 69114, Bukit Kretam, Sandakan District, Sabah; FMNH 77563, Kalabakan, Tawau District, Sabah; FMNH 140242, Kota Kinabalu District, Sabah; FMNH 83026, Long Akah, Akah River, Fourth Division, Sarawak; FMNH 77576, Nanga Putai, Baleh River, Seventh Division, Sarawak; FMNH 96018–20, 167996, headwaters of Baleh River, Seventh Division, Sarawak; FMNH 216169–71, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Rhacophorus kajau Dring

Assignment of these larvae to adults was based upon discovery of a clutch of eggs in an area occupied by a calling aggregation observed by Dring (1983b) on two successive nights. Two were reared to late Stage 25.

Description—**External**—Similar to larval *R. appendiculatus.* Head-body width .75 of head-body length; eyeball .13 of head-body length; interorbital .29 of head-body width; tail length 1.9 times head-body length. Interorbital less than twice diameter of eyeball; lower lip with single continuous row of papillae; denticles I:3+3/1+1:II; tail with convex margins, tapering to narrow tip. Head-body with faint dark spots and a dark band across rear; caudal muscle with dark spots; dorsal fin with dark spots proximally; rest of fins without pigment. Head-body length 5.8–6.0 mm (Stage 25).

Ecological Distribution—The group of eggs, which, according to Dring, were not in a foam mass but in a single layer, was attached to a leaf overhanging a pool of an intermittent stream.

Referred Material—BMNH 1978.1764, Mt. Mulu National Park, Fourth Division, Sarawak.

Rhacophorus sp. D

Association with any species of adult is not possible because the most advanced tadpole is in Stage 27. The general habitus and form of the oral disk

are ranoid. The number of upper rows of denticles (4) and the continuous double row of papillae on the lower lip eliminate assignment to the *Rana blythi-kuhli* complex, and the lack of patches of glands eliminates the *Rana* (*Hylarana*) complex. These tadpoles appear most similar to larval *Rhacophorus,* but differ from most other Bornean forms of that genus (but not *harrissoni*) in the dark, patternless coloration and in the small number (2) of rows of denticles on the lower lip. The relative immaturity of these tadpoles casts some doubt on the validity of the last distinction, although in other larval *Rhacophorus,* the full complement of denticles appears in Stage 25. The Bornean species of *Rhacophorus* from lowland forest whose larvae have not been described are *R. fasciatus* and *rufipes.* One adult of *R. fasciatus* was collected at the locality from which these larvae came.

DESCRIPTION—**External**—Head-body broadly oval, snout obtusely pointed; maximum body width between eye and end of body, .66–.72 of head-body length, depth .75–.80 of width; eyes dorsolateral, not visible from below, eyeball .08 of head-body length (Stages 25–27); interorbital .30 of head-body width, about equal to eye–snout distance; nostrils dorsolateral, open, rim not raised; nasolacrimal duct not evident. Oral disk ventral, subterminal, width .33–.39 of head-body width; lips thick, sharply raised above surrounding area of snout; lower lip with staggered, continuous double row of short papillae; similar papillae confined to corners of upper lip; denticles I:3+3/1+1:I; beaks finely serrated; narrowly edged with black, upper without median convexity. Spiracle sinistral, midway up side, tube fused to body wall, opening slightly constricted, snout–spiracle .56–.59 of head-body length. Anal tube dextral, opening not reaching margin of fin. Tail with both margins convex, tapering to rounded tip, 1.7–2.0 times head-body length, maximum depth .30–.39 of tail length; origin of dorsal fin above end of body, deeper than caudal muscle beyond proximal third, deeper than ventral fin throughout. Lateral line pores on side of snout and around eye and dorsolaterally to end of body and along middle of caudal muscle.

Color in preservative entirely dusky gray, no pattern.

Head-body length of largest in Stage 25, 7.3 mm; in Stage 27, 9.0 mm. Total length at Stage 27, 24.0 mm.

The denticles are similar to those of other *Rhacophorus* larvae, spatulate, with rounded apex, curved margins and with 14–16 wide, pointed cusps around the distal half of the shaft.

Internal Buccopharyngeal (based on FMNH 158031, Stage 26, examined by means of SEM)—Prelingual area of floor bordered posterolaterally by 3 thick papillae; middle one of each set largest, with 3 stubby, pustulose branches; inner one shortest, with 3 pustules, separated from one of other side by distance equal to height of one; anterolateral papilla with short apical projections; anterior to these a transverse row of 3–5 pustules separated by wide median gap from row on other side. Tongue anlage not raised at this stage; 2 thick, conical lingual papillae widely separated; distance between them equal to distance between median prelingual papillae. Buccal roof arena with 6 conical papillae in a double row on each lateral border; the second papilla tallest and with several pustules; about 30 pustules in posterior two-thirds of interior of arena and on dorsal surface of velum; a group of 6–8 pustules around anteriormost lateral papilla. Buccal pockets narrow, curved, oblique. Ventral velum supported by spicules; no median notch; margin undulant, without distinct projections; secretory pits present on margin. Glottis obscured in preparation. Branchial baskets with 3 oblique gill chambers; filter ruffles with tertiary folds; filter canals open.

Prenarial area of roof with curved, transverse row of 3 pustulose, truncate projections; 1 or 2 small pustules laterally on each side. Nares transverse, oval, separated by about half length of one; anterior narial wall low, with slight elevation medially and a short, medially curved papilla rising from lateral third; posterior narial wall thin, with a low median expansion. Postnarial area with a distinct depression behind each naris; a large, thick, pustulose, medially projecting papilla behind median third of depression, 2 or 3 low pustules behind lateral half of depression. Lateral ridge papilla tall, slender, with several pustules near apex. Median ridge wide, tapering abruptly above base to parallel-sided, truncate extension; margin with short projections or pustules; height greater than width. Buccal roof arena with many low, evenly spaced pustules. Glandular zone deep, continuous across roof. Dorsal velum weakly undulant, margin with secretory pits.

ECOLOGICAL DISTRIBUTION—The single sample of 15 tadpoles was taken from a rain pool formed in a depression of a large, flat rock.

REFERRED MATERIAL—FMNH 158030–1, Sungei Pesu, Tubau district, Fourth Division, Sarawak.

Rhacophorus bimaculatus Group

Three of these four larval forms are sympatric at Nanga Tekalit, Sarawak, and though occurring in the same small streams, appear to be ecologically isolated from one another (see each species account). One of them is sympatric and, possibly, syntopic with the fourth form in streams on Mt. Kinabalu. Premetamorphic larvae have fingers extensively webbed and well developed, round disks on all digits, a combination of characters found only in *Rhacophorus* among genera known from Borneo. Calling males of *R. bimaculatus* and *R. gauni* have been collected over a 22-year period from vegetation lining the banks of the streams where three forms were found at Nanga Tekalit. Although the developmental series do not extend far enough to reveal diagnostic features of adults (other than webbing and disks), it is reasonable to assign two of the larval types to *bimaculatus* and *gauni,* at least provisionally. The one I assign to *bimaculatus* is the one recorded from Nanga Tekalit and Mt. Kinabalu. Adults of this species have been collected at both localities. This larva was mistakenly referred to *Staurois latopalmatus* in a previous paper (Inger, 1966). The larval form assigned to *R. gauni* was caught mainly in leaf drifts that accumulate below riffles. A small foam nest containing 21 embryos was found hanging from a branch drooping over a riffle, and we subsequently heard *gauni* calling from the same small tree.

If we assume that these two species of small tree frogs are indeed the parental species of two of these larval forms, there remains the issue of parental species of the other two. Only three additional Bornean species of *Rhacophorus* are not represented by known larvae: *baluensis, everetti,* and *rufipes.* Calling males of the first and last have been seen at isolated forest pools (field notes of J. Dring and Inger), and consequently, they are not likely to have tadpoles that live in permanent streams. Habitat distribution of *everetti* is unknown, but it and *baluensis* have been collected on Mt. Kinabalu, the locality for one of the unnamed larvae.

Although all four forms have specialized oral disks, they vary in degree and manner of divergence from the typical ranoid pattern. Larval *R. bimaculatus* have the most derived beaks, which are ribbed, coarsely serrated, and fully pigmented. It also has a continuous row of papillae across the upper lip, another derived feature, but its denticular formula is the least divergent (II:2+2/1+1: II). The second form from Mt. Kinabalu (designated sp. KB below) also has papillae on the entire margin of the upper lip and a slightly more divergent denticular formula on the lower lip (V). Its beaks are more like the usual ranoid style, both being smooth on the outer surface, though the upper one is coarsely serrated. The form designated *Rhacophorus* sp. NT has a more divergent denticular formula on the upper lip (II:4+4 or II:5+5), but typical ranoid beaks (i.e., smooth on outer surfaces, finely serrated margins) and papillae restricted to the lateral fifths of the upper lip. Larval *R. gauni* have typical ranoid beaks and papillae missing only from the medial third of the upper lip. They have the most derived denticular formula on the upper lip (IV:5+5 or IV:6+6).

The buccopharyngeal morphology of this group of larvae also has derived features, if we assume that the states common to larval *Rana, Polypedates,* and *Rhacophorus* represent the primitive conditions. Larvae of the last three genera have 2 or 4 lingual papillae, a well-defined buccal floor arena marked by rows of lateral papillae and many interior pustules, 9–12 filter rows on the medial wall of the middle gill chamber, a low anterior narial wall, and a well-defined buccal roof arena marked by 3–7 lateral papillae and many interior pustules. Larval *Rhacophorus bimaculatus* lack lingual papillae, have few pustules in the interior of the buccal floor and roof arenas, and have the anterior narial wall drawn out into an anteriorly projecting flap pressed against the roof. Larval *Rhacophorus gauni* have the same odd modification of the anterior narial wall and no lingual papillae. In addition, their buccal floor and roof arenas are poorly defined, being completely devoid of interior pustules and lateral papillae, except for 1 papilla in the floor arena. They have 16 filter rows on the median wall of the middle gill chamber. Larval *Rhacophorus* sp. NT have a typical ranoid buccopharyngeal cavity, except in one respect: they have 15 filter rows in the middle gill chamber. Larval *Rhacophorus* sp. KB were not dissected.

Rhacophorus bimaculatus (Peters)

Association of these larvae with adults is discussed above. Specimens range from Stages 25 to 41. Tadpoles in the last stage have extensively webbed fingers and enlarged, round finger disks.

DESCRIPTION—**External**—Head-body ovoid, snout broadly rounded, flattened below, maximum width between eye and end of body, .55–.61 of head-body length, depth .66–.82 of head–body width; eyes dorsolateral, not visible from below, eyeball .10–.12 of head-body length (Stages 36–38); interorbital about twice eye diameter, .33–.37 of head-body width; nares lateral, midway between eye and tip of snout; internarial slightly narrower than interorbital. Oral disk ventral, cuplike, width .74–.83 of head-body width; both lips with complete fringe of slender, short papillae; upper lip with single row of short, thick inframarginal papillae medially and 2–3 rows laterally; lower lip with 4–5 rows of similar papillae between denticles and margin of lip. Denticles II:2+2/1+1:II; all rows extending full width of lips; denticles in outermost rows of both lips about half height of those in other rows; gap between halves of lower divided row distinct; denticles of all rows decreasing in size from center outward. Beaks heavy, V-shaped, fully pigmented; surface of both ribbed; margins with coarse serrae, 18–22 on upper, 15–28 on lower; transverse width of beaks subequal. Spiracle low on left side, tube free of body wall near end, snout–spiracle .65–.78 of head-body length. Anal tube median, detached from ventral fin near tip. Tail narrow, dorsal margin weakly convex, tapering in distal third to rounded tip; tail length 1.7–1.9 times head-body length, maximum depth .24–31 of tail length. No glands or lateral line pores visible. In preservative head-body light brown above and laterally, colorless below; caudal muscle with brown spots; dorsal fin mottled.

Head-body lengths (mm): 5.2–7.3 (Stages 26–29), 6.9–7.8 (Stages 30–33), 7.1–9.1 (Stages 34–37), 9.0–9.1 (Stages 38–41). Total length to 24.9 mm (Stage 37).

The denticles are scoop-shaped, with many short, closely set marginal cusps. The shaft is sharply bent toward the mouth, making an acute angle.

Internal Buccopharyngeal (based on FMNH 83020, Stage 36)—Prelingual area of floor with a long, fringed ridge on each side oriented anterolaterad–posteromesad, extending from rear of prelingual forward two-thirds of distance to corner of lower beak, fringe composed of many conical papillae set on continuous, raised, narrow base; 3 short papillae on each side mesad from ridge; first simple, conical, opposite anterior end of ridge; second pustulose and taller than first; third bi- or trifid, near rear of ridge. Tongue anlage raised, oval, without papillae. Buccal floor arena oval; a staggered row of 9 or 10 papillae on each lateral border; interior of arena with 3 pustules posteriorly; 3 or 4 pustules lateral to last 3 lateral papillae. Ventral velum supported by spicules; margin with 7 short, thick papillae on each side; no secretory pits visible on dorsal surface. Glottis completely exposed behind velum. Branchial baskets relatively small, not extending much behind velum; filter canals open.

Prenarial area of roof without projections; beak set in a large swelling. Nares oval, widely separated; anterior narial walls confluent anteromedially, forming long, narrow, flat flap reaching rear of prenarial swelling, flap with 2 or 3 very short pustules at tip; posterior narial wall thin, without pustules or papillae. Postnarial area with 7 tall, slightly curved papillae forming a slightly oblique U behind each naris; the anteromedial papilla behind center of narial wall and at same level as median ridge, but well separated from the latter. Lateral ridge papilla not distinguishable. Median ridge tall, slender, with a few marginal pustules. Buccal roof arena with 2 or 3 slender papillae on each lateral border; interior with a short, conical papilla anteriorly and 7 pustules posteriorly. No evident glandular zone. Dorsal velum with marginal papillae similar to those of ventral velum.

ECOLOGICAL DISTRIBUTION—Largely limited to those parts of streams having moderate to strong current. In addition to the samples from the Seventh Division, Sarawak, whose microhabitat distribution is shown in Table 22, we have 4 small samples from Mt. Kinabalu at elevations between 550 and 790 m in portions of streams that included riffles, pools, and low waterfalls. The sample from the highest elevation was collected with 3 larvae of *Rhacophorus* sp. (Kinabalu) and 2 larvae each of *Amolops* sp. F and *Leptobrachella mjobergi*. Another of the Kinabalu samples was taken with larval *Amolops* sp. F, a third with larval *Amolops* sp. E, and the fourth without other forms.

REFERRED MATERIAL—FMNH 130921–22, 130924, Sungei Mamut, Mt. Kinabalu, Sabah; FMNH 213128, Sungei Kepungit, Mt. Kinabalu, Sabah; FMNH 83020, Long Seniai, Akah River, Fourth Division, Sarawak; FMNH 77523–4, Sungei Entunau, Baleh River, Seventh Division, Sarawak; FMNH 213888–96, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Rhacophorus gauni Inger

Association with this species is tentative for the reasons given above (p. 81). The sample spans Stages 26–41.

TABLE 22. Microhabitat distribution of larval *Rhacophorus bimaculatus* in forest streams and their occurrence with tadpoles of other species.

Species	No. of samples			
	Torrent	Riffle	Shingle	Protected side pool
Leptobrachella mjobergi	...	1	2	...
Leptobrachium gracilis	...	2	...	...
Leptobrachium montanum	...	1	2	...
Megophrys nasuta	1	3	4	...
Amolops phaeomerus	1	1	...	...
Amolops poecilus	1	1	2	...
Rana chalconota	...	...	1	1
Rana ibanorum	...	...	1	1
Rana signata	...	1	...	1
Without other tadpoles	2	0	0	0
Total samples	3	4	7	2

DESCRIPTION—**External**—Head-body ovoid, snout broadly rounded, body flattened above and below, maximum width midway between eye and spiracle, .58–.61 of head-body length, depth .67–.72 of width; eyes dorsolateral, not visible from below, eyeball .10–.11 (Stages 29–34), interorbital .35–.42 of head-body width; nares dorsolateral, closer to eye than to tip of snout, internarial subequal to interorbital. Oral disk ventral, cuplike, width .70–.81 of head-body width; lower lip with 3–4 complete rows of short papillae; upper lip with a marginal row of short papillae except in median third and a second inframarginal row laterally. Denticles IV:5+5 or IV:6+6 on upper lip, 1+1:II or III on lower lip; denticles of outermost row on lower lip and of 3 outermost rows on upper lip much smaller than those of other rows; within each row denticles decreasing in size from center outward. Beaks relatively weak, pigmented only along marginal third; upper pigmented only in median half; outer surface of both smooth; both beaks finely serrated and gently curved; lower beak much wider than upper. Spiracle low on side, tube free of body wall near tip for distance equal to its diameter, snout–spiracle distance .75–.80 of head-body length. Anal tube dextral, attached to ventral fin entire length. Tail narrow, margins weakly convex, tapering gradually in distal third to narrow rounded tip; tail length 2.1–2.4 times head-body length, maximum depth .23–.26 of tail length; origin of dorsal fin separated from end of head-body; fins subequal, neither as deep as caudal muscle until distal fourth. No glands or lateral line pores visible. In preservative head-body black dorsally and laterally; caudal muscle black, fins without pigment except next to muscle in stages beyond 31.

Head-body lengths (mm): 5.25–7.3 (Stages 26–29), 7.1–8.3 (Stage 31), 8.5 (Stages 34–35), 10.0–10.4 (Stages 41–42). Total lengths to 35.4 mm (Stage 41).

Internal Buccopharyngeal (based on FMNH 221584, Stage 35)—Prelingual area of floor with 2 compressed, anteroposteriorly oriented flaps on each side; each flap with 3–4 short marginal projections. Tongue anlage low, wider than long, pointed at rear; no lingual papillae. Buccal floor arena poorly defined, a single long papilla laterally; interior without pustules. Buccal pockets oblique, wide; 7 widely spaced prepocket pustules. Ventral velum supported by spicules; margin with 6 short, thick projections on left side, 3 more widely spaced ones on right; secretory pits not visible. Glottis behind velum. Branchial baskets large, extending well behind velum; 3 gill chambers on each side; 16 filter rows on median wall of middle chamber; filter canals open.

Prenarial area of roof with transverse, pustulose ridge in center. Nares round, widely separated; narial walls drawn out medially into large, anteriorly directed, narrow flap separated from one of other side. Postnarial area with a single, large, pustulose papilla behind median third of each naris. Lateral ridge papilla curved, not as tall as postnarial. Median ridge tall, slender, height twice base, margin smooth. Buccal roof arena ill-defined, without projections. Glandular zone only a few pits deep, but extending across roof. Dorsal velum damaged in dissection.

ECOLOGICAL DISTRIBUTION—This form is restricted to leaf drifts (7 samples) and open pools

(1). In leaf drifts it was collected with larval *Ansonia longidigita* (6 samples), *Pedostibes hosei* (3), *Rana blythi* (5), *R. signata* (2), *R. chalconota* (1), and *Leptobrachium montanum* (2).

REFERRED MATERIAL—FMNH 213887, 221576–84, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Rhacophorus sp. NT

Association with any species of adults is not possible.The developmental series, Stages 27–39, stops short of a point at which diagnostic features might be present.

DESCRIPTION—**External**—Head-body ovoid, snout rounded, body flattened above, rounded below, maximum width midway between eye and end of body, .64–.70 of head-body length, depth .69–.79 of width; eyes dorsolateral, not visible from below, eyeball .12–.14 of head-body length (Stages 27–39); interorbital about 1.5 times diameter of eye, .30–.36 of head-body width; nares dorsolateral, slightly closer to tip of snout than to eye, internarial subequal to interorbital. Oral disk ventral, subterminal, width .40–.49 of head-body width; lower lip with 3 complete rows of short papillae; upper lip with a double row of short papillae in lateral thirds. Denticles II:4+4 or II:5+5 on upper lip, 1+1:II on lower lip; denticles in outermost row of both lips distinctly smaller than those of adjacent rows; within each row denticles decreasing in size from center outward. Beaks moderate, pigmented along marginal half; outer surfaces smooth; margins finely serrated; both beaks gently curved; beaks subequal in transverse dimension. Spiracle low on side, tube completely fused to body wall, snout–spiracle distance .54–.61 of head-body length. Anal tube dextral, attached to ventral fin entire length. Tail with weakly convex margins, tapering gradually in distal two-thirds to narrow tip; tail length 1.6–1.9 times head-body length, maximum depth .31–.37 of tail length; origin of dorsal fin at end of body; dorsal fin deeper than ventral except in distal fourth, deeper than caudal muscle in distal two-thirds. No glands visible. Lateral line pores conspicuous; in 2 rows from snout, 1 above nostril and eye and 1 below; rows joining behind eye for short distance, then separating into dorsal and dorsolateral rows, the upper extending onto dorsal fin and the lower onto center of caudal muscle. In preservative head-body light gray dorsally and laterally; usually a dark vertical bar below rear of eye and a longer horizontal one on side of snout; caudal muscle gray, fins with lighter dusting of melanophores.

Head-body lengths (mm): 9.3–9.6 (Stages 27–29), 9.2–10.8 (Stages 31–32), 10.9–11.8 (Stages 35–36), 12.6–13.2 (Stages 37–39). Total lengths to 37.3 mm (Stage 38).

Internal Buccopharyngeal (based on FMNH 221571, Stage 36)—Prelingual area of floor with 3 pairs of pustulose papillae; a median pair of short papillae across rear of area, a tall papilla in each posterolateral corner, and a short one in each anterolateral corner; a low transverse row of pustules just anterior to anterolateral papillae. Tongue anlage raised, wider than long; 2 very short lingual papillae. Buccal floor area wide, pentagonal; bordered laterally by 5 (right side) or 6 papillae, all pustulose at tips; second and fourth on each side tallest; fourth on left branched near base; 20 widely spaced pustules in a band across rear third of arena, extending lateral to papillae. Buccal pockets transverse, curved. No prepocket papillae. Ventral velum supported by spicules; margin with 7 short projections on each side, medial 3 close together; no secretory pits visible. Glottis completely exposed behind velum; in a raised disk. Branchial baskets moderate in size; 3 chambers on each side; filter ruffles dense, complexly folded; 15 rows of filters on median wall of middle gill chamber; filter canals open.

Prenarial area of roof with a long, U-shaped, pustulose ridge, open to the rear. Nares transverse, separated by half length of one; anterior narial wall low, pustulose, with short papilla in lateral third; posterior narial wall taller, smooth, medially drawn out into a short valvular flap, no papilla. Postnarial area with 1 tall, medially curved papilla behind middle third of each naris; papilla with pustules on anterior margin. Lateral ridge papilla tall, but not as long as postnarial. Median ridge triangular, taller than wide, margin with 5 short projections. Buccal roof arena with 5 papillae on left border and 7 on right, first in each series longest and with several pustules near tip; interior with 35 low pustules widely and irregularly spaced. Glandular zone present, damaged in dissection. Dorsal velum also damaged.

ECOLOGICAL DISTRIBUTION—Appears to be very restricted. All 7 samples were obtained in potholes on rocky banks of streams in association with larval *Microhyla petrigena* (3 samples), *Ansonia longidigita* (2), *Rana blythi* (3), *R. chalconota* (4), *R. ibanorum* (2), *R. ingeri* (1), and *R. signata* (1).

REFERRED MATERIAL—FMNH 221565–75,

Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Rhacophorus sp. KB

Association of these tadpoles with adults is not possible now. All 6 samples are from the slopes of Mt. Kinabalu where this form is at least partly syntopic with larval *Rhacophorus bimaculatus*. They differ from the latter in relative sizes of beaks, denticular formula, and coloration. The oldest larva (Stage 39) has the outer fingers half-webbed.

DESCRIPTION—**External**—General form of body and oral disk as in *R. bimaculatus*. Head-body width .61–.64 of head-body length, depth .69–.71 of width; eyeball .11–.13 (Stage 27), .14 (Stage 39) of head-body length; tail length 1.8–2.0 times head-body length, maximum depth .28–.40 of tail length. Maximum body width just behind eyes. Lips with complete fringe of slender marginal papillae; upper lip with a double, staggered row of low, thick, inframarginal papillae. Denticles II:2+2 on upper lip; 1+1:III (3 larvae, Stages 25–27), IV (4 larvae, Stages 26–30), or V (3, Stages 27–39) on lower lip. Beaks V-shaped; upper fully pigmented medially, without pigment laterally; lower beak pigmented in marginal half; pigmented portion of upper beak about half transverse width of lower; outer surface smooth; upper beak with 14–17 coarse serrae, lower with many fine ones. Spiracle low on side, tube free of body wall most of its length. Anal tube dextral, attached to ventral fin. In preservative head-body light brown above and on sides; caudal muscle dusky, with indistinct darker spots; dorsal fin with 3 or 4 intense dark spots at margin; ventral fin usually with a dark marginal spot near tip.

Head-body lengths (mm): 7.7–9.3 (Stages 26–27), 9.8 (Stage 30), 12.8 (Stage 39). Total length to 35.3 mm (Stage 39).

ECOLOGICAL DISTRIBUTION—Poorly defined because field notes lack precision. All, however, are from streams at 790–1,160 m. Two of the samples appear to be from riffles, and the others, from sections of streams consisting of pools, riffles, and low falls. Information on association with other kinds of tadpoles is marred by the same lack of precision with respect to microhabitats. These general samples include larvae of *Leptobrachella mjobergi, Leptobrachium gracilis, L. montanum, Ansonia* sp., and *Rhacophorus bimaculatus*.

REFERRED MATERIAL—BMNH 1976.2283, Sungei Silau Silau; FMNH 130918–20, Sungei Kepungit; FMNH 131249–50, Sungei Liwagu. All from Mt. Kinabalu, Sabah.

Nyctixalus pictus (Peters)

Association of these larvae with *N. pictus* is based on two developmental series, each including a metamorphosing individual having the distinctive dorsal spinules and bicolored digital disks of adult *pictus*.

DESCRIPTION—**External**—Head-body oval, almost circular in early developmental stages, snout broadly rounded; maximum width just behind eyes, .64–.79 of head-body length; flattened above, depth .60–.75 of width; eyes dorsal, eyeball .05–.06 of head-body length (Stages 25–31), .15 (Stage 42); interorbital .29–.31 of head-body width, about three-fourths of eye–snout distance; nostrils dorsal, open, a small projection from the rim middorsally; internarial slightly narrower than interorbital; nasolacrimal duct obscured in premetamorphic stages. Oral disk terminal, ventral, width .36–.44 of head-body width; slender, short papillae in staggered double row across lower lip, usually without a median gap; crowded papillae at corners of upper lip; denticles I:4+4/III or II:3+3/III; beaks with fine, long serrations, black in marginal half; upper beak with weak median convexity. Spiracle sinistral, low on side, tube attached to body wall, snout–spiracle .64–.74 of head-body length. Anal tube median. Tail weakly convex, tapering gradually to broadly rounded tip; length 1.3–1.5 times head-body length, maximum depth .34–.36 of tail length; caudal muscle deeper than either fin in proximal two-thirds; origins of fins at end of body, dorsal fin deeper than ventral in proximal half. Lateral line pores conspicuous dorsally and ventrally on head-body and along center of caudal muscle.

Entire tadpole dark brown, lighter ventrally on head-body, fins lighter than caudal muscle.

Head-body lengths (mm): 15.0–17.5 (Stage 26), 18.3 (Stage 31), 17.1 (Stage 42). Total length to 43.3 mm (Stage 26).

Internal Buccopharyngeal (based on FMNH 157755, Stage 26)—Prelingual area of floor posterolaterally with a large, flattened, branched palp; directly anterior to palp 1 thick papilla bearing 2 pustules; 1 pustule anterior to papilla on right side only; a median pair of low papillae between palps. Tongue anlage low; 4 tall, slender lingual papillae. Buccal floor arena hexagonal; 5 papillae in curved staggered row in anterior half of each lateral border, third and fifth papillae branched; about 12 conical papillae in a triangular group at each posterolateral corner; interior occupied by 25 low,

evenly spaced pustules. Buccal pockets wide, curved, not perforated; 8–10 short, conical papillae anterior to each pocket. Ventral velum supported by spicules; median area indented, but not notched; margin wavy, 1 short projection on each side. Glottis exposed. Three gill chambers on each side, but inner one miniscule and far medial; filter mesh dense; 13 filter rows on medial wall of middle chamber.

Prenarial area of roof with transverse, pustulose, angular ridge; a pair of short papillae anterior to ridge; 1 pustule lateral to papilla on right side. Nares transverse, long, narrowly separated; anterior wall raised, with papilla rising from lateral third; posterior narial wall valvular with rounded expansion in center. Postnarial area with a tall, pustulose papilla behind median third of naris; 2 low pustules in area behind papilla. No lateral ridge papilla. Median ridge a narrow, truncate triangle, height twice width of base, margin pustulose. Buccal roof arena with 12 conical papillae in posterior half of each lateral border, first 3 in single file, others in curved double row; interior of arena with 40–50 low, evenly spaced pustules. Glandular zone extending across roof, narrowed medially. Dorsal velum damaged in dissection.

Ecological Distribution—Restricted to water-containing holes in tree trunks and logs. A group of eggs was found attached to the wall of a tree cavity above the small pool of water it contained; 2 tadpoles were reared from this sample to Stage 25, at which point they have the peculiar circular body form and relatively short tail. Another sample of 15 eggs was seen about 7 cm above water in a second tree hole; 4 of these eggs were removed for rearing and tadpoles preserved at various stages. Neither cluster of eggs was associated with foamy mucous, and in both instances each egg was encased in a large amount of gelatin. A third sample of 4 tadpoles was removed from a hole in a log; this appeared to be the entire complement. No tadpoles of other species were found with these samples.

Referred Material—FMNH 157752–3, 157996, Labang, Kemena River, Fourth Division, Sarawak; FMNH 157755–6, 157999–8001, 158032, Sungei Pesu, Tubau district, Sarawak.

Rhacophorid (Genus?)

Association of these 5 young tadpoles (most advanced in Stage 32) with any adult is not possible. As they were found in a water-filled plastic cup fixed to a tree at 1 m above ground, an artificial tree hole, it is almost certain that they are rhacophorid larvae. They are not like any other known Bornean rhacophorid tadpole. However, their terminal mouth, reduced denticles, dorsally situated eyes, heavy and fully pigmented beaks, and small branchial baskets recall another tree hole tadpole of Southeast Asia, *Philautus* sp. (cf. *carinensis*) (Wassersug et al., 1981). In many of these features, they also resemble the bromeliad-dwelling neotropical *Hyla zeteki*. Both of the last appear to feed exclusively on anuran eggs, while the present form does not. Its gut has numerous coils packed, in these specimens, with dark material. Identifiable fragments, in a smear made from 1 sample, comprise pieces of chitin (bristles, etc.) and stomate plant tissue.

Morphological differences from *Philautus* sp. (cf. *carinensis*) in detail are extensive. The *Philautus* larva has many (ca. 150) papillae on the lips; the Bornean form has no papillae, but a few scallops confined to the lower lip. The *Philautus* larva has a row of about 50 tall denticles on the upper lip and none on the lower; the present form has a single, divided row of 6–13 small denticles on the lower lip only. Internally, the *Philautus* larva has 1 cylindrical prelingual papilla, no lingual papillae, no prenarial projections, small postnarial papillae, and no median ridge. The Sarawak tadpoles differ on each of these points (see below).

Description—**External**—Head-body oval, somewhat elongate; snout obtusely pointed; maximum width of head-body at level of eyes, narrowing abruptly anterior to eyes to narrow snout; head-body width .58–.63 of head-body length, depth .71–.84 of width; eyes dorsal, pointing up and out, eyeball .09–.11 of head-body length (Stages 29–32); interorbital .37–.40 of head-body width, subequal to eye–snout distance; nostrils dorsolateral, open, rim not raised, internarial slightly less than interorbital; nasolacrimal duct not evident. Oral disk terminal, slightly ventral, width .33–.37 of head-body width; lips narrow; margin of lower lip scalloped rather than papillate; upper smooth; denticles limited to 1 short, widely interrupted row on lower lip, 3–7 denticles in each half; denticles do not appear to project above surface of lip (at 50×); no denticles on upper lip; beaks very robust, fully pigmented, lower coarsely serrated and V-shaped, upper smooth and with weak median notch. Spiracle sinistral, low on side, tube fused to body wall, snout–spiracle .48–.57 of head-body length. Anal tube dextral. Tail with almost straight margins, tapering gradually in distal half to narrow tip; length 2.0–2.3 times head-body length, max-

imum depth .24–.25 of tail length; caudal muscle deeper than fins except in distal fourth; origin of dorsal fin at end of body; fins subequal in depth. No lateral line pores visible.

Head-body, caudal muscle, and dorsal fin finely dusted with melanophores in preservative; ventrally melanophores confined to anterior half of body.

Head-body lengths 6.8–7.4 (Stages 29–32). Total length to 24.1 mm.

Internal Buccopharyngeal (based on FMNH 214718, Stage 32)—Preservation was poor, limiting observation. Prelingual area of floor with a large flattened palp, taller than wide, in each posterolateral corner; apex with 2 unequal projections; a pair of short, thick papillae between palps medially, papillae separated by twice their thickness. Tongue anlage low; 2 lingual papillae in center, height 1.5 times that of median prelingual papillae. Buccal floor arena with 3 thick papillae in posterior half of each lateral border; interior smooth. Rest of floor obscure. Branchial baskets small; there appear to be only 2 chambers.

Prenarial area of roof with a large transverse flap occupying median third or fourth in center, height subequal to width, apex with a short conical projection in each corner and a wide rectangular projection in middle. Nares oval, transverse, narrowly separated; anterior narial wall pustulose medially, with a short conical papilla laterally; posterior narial wall thin, with a weak expansion medially. Postnarial area with a sharply defined depression behind each naris; a tall postnarial papilla rising from near edge of depression behind middle of naris, papilla with 2 or 3 apical pustules. Lateral ridge papilla simple, conical, subequal to postnarial papilla. Median ridge about as high as wide, tip rounded, margin with 3 pustules. Buccal roof arena narrow, with 2 thick, conical papillae in each lateral border. Interior of roof arena and area behind it damaged.

ECOLOGICAL DISTRIBUTION—See above.

REFERRED MATERIAL—FMNH 214718, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

Ranoid Larva, Genus Unknown

Association of this sample of 3 small tadpoles (maximum head-body length 6.5 mm) with any species of adults is not possible. All are in late Stage 25 and have fully developed oral disks. The beaks and denticles are unlike those of pelobatid larvae, and the number of rows of denticles is much greater than that of any Asian bufonid larva. In fact, the denticular formula is unique among Bornean tadpoles. Although a few larval *Amolops* and *Leptobrachium* have as many rows (7) on the lower lip, all of those tadpoles have at least 6 on the upper lip, whereas the unnamed form has only 2. The depressed head-body is another distinctive feature of this form. The eyes are very small (.04–.05 of head-body length), but that may merely reflect the early stage of development rather than another specialization (see *Leptobrachium gracilis,* p. 9). None of the external characters eliminate either Ranidae or Rhacophoridae as the home family. The denticular formula is so unusual that it prevents association with any of the known larval groups of those two families.

Two riparian species groups occurring at Nanga Tekalit, Sarawak, where these tadpoles were collected, are not represented by identified larvae: *Rana hosei* and *Staurois* (three species). Females of both groups have nonpigmented ova, which hints at specialization of oviposition. The tadpoles were collected in a leaf drift with larval *Leptobrachium montanum, Pedostibes hosei, Ansonia longidigita, Rana blythi,* and *Rhacophorus gauni.* Ripe ova of the last three lack the intense pigmentation common to anuran ova. While these observations do not constitute proof of association of the unknown larvae with either *Rana hosei* or *Staurois,* the character of the ova of those two groups makes them likely parental stock.

DESCRIPTION—**External**—Head-body oval, depressed, snout rounded, maximum width between eye and spiracle, .60–.63 of head-body length, depth .58–.62 of width; eyes dorsal, pointing outward, eyeball .04–.05 of head-body length (Stage 25); interorbital 3–4 times diameter of eye, .24–.33 of head-body width; nares lateral, open, closer to tip of snout than to eye, internarial wider than interorbital. Oral disk ventral, subterminal, width .52–.54 of head-body width; lips not expanded, papillae short homogeneous, in single uninterrupted marginal row across lower lip and at corners of upper lip. Denticles I:1+1/1+1:VII, the 3 outermost rows of lower lip shorter than others and consisting of very small denticles. Beaks with narrow marginal black strip; very finely serrated; upper sinuate with median indentation. Spiracle sinistral, midway up side; tube free of body wall at tip; snout–spiracle distance .73–.81 of head-body length. Anal tube dextral, opening near margin of fin. Tail narrow, margins weakly convex, tapering slightly to broadly rounded tip; length 1.9–2.1 times head-body length; maximum depth .25–.27 of tail

length; caudal muscle deeper than either fin in proximal three-fifths; dorsal fin origin just behind head-body, rising very gradually, not as deep as ventral fin in proximal three-fifths. No glands or lateral line pores visible. In preservative pale gray; fine dusting of melanophores dorsally on head-body and caudal muscle; no melanophores on fins, laterally or ventrally on head-body, or ventrally on caudal muscle.

Head-body lengths of 3 in Stage 25, 5.4–6.5 mm. Total lengths to 19.5 mm.

ECOLOGICAL DISTRIBUTION—See above.

REFERRED MATERIAL—FMNH 221024, Nanga Tekalit, Mengiong River, Seventh Division, Sarawak.

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